LOWER CRETACEOUS TRIGONIOIDA (MOLLUSCA, BIVALVIA) FROM THE ALGOA BASIN, WITH A REVISED CLASSIFICATION OF THE ORDER

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(With 25 figures)

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ABSTRACT

The diversity of trigonioid bivalves makes their assignment to a single family inappropriate. On phyletic grounds it is proposed to recognize the suborders Trigoniina and Myophorellina nov. to include the superfamilies Myophoriacea Bronn, Trigoniacea Lamarck, Myophorellacea Kobayashi, and Megatrigoniacea van Hoepen. In addition, the following new taxa are introduced: family Gruenewaldiidae, subfamily Steinmanellinae, tribe Heterotrigoniini, and genera *Skwarkoella* and *Lambertiella*.

The late Valanginian trigonias of the Sundays River Formation, last reviewed as a group in 1908, are revised and shown to comprise 11 species in seven genera (*Trigonia*, *Myophorella*, *Steinmanella*, *Iotrigonia*, *Megatrigonia*, *Pisotrigonia* and *Pterotrigonia*). These taxa represent six subfamilies in four families.

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INTRODUCTION

The trigonioid bivalves comprise a generally highly ornate group of infaunal burrowers that dominated Mesozoic shallow-marine environments. They display a bewildering and unsurpassed diversity of morphology that, because of a strong substrate control, involves rampant homoeomorphy and parallel evolution. Relationships have been further obscured by a general failure to appreciate that in each region evolution occurred in isolation for long periods of time, punctuated by periodic regional interchange (at times of high sea-level) and

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faunal replenishment. As a result, although there are general similarities between the trigonioid faunas of different regions, species are almost invariably endemic and are descended from and most closely related to species from the same region. Consequently, a conservative taxonomy (cf. Cox 1969) and attempts to apply a few well-established names to taxa from different regions has served merely to obscure and confuse the phylogeny of the group, and to mask one of the great radiations in the animal world.

Trigonioid bivalves are particularly well represented in the Sundays River Formation of the Uitenhage Group (Goldfuss 1837; Krauss 1843; Sharpe 1856; Holub & Neumayr 1881; Kitchin 1908; Pringle 1960; Cooper 1979*a*). This fauna was last revised as a group in 1908, when only the genus *Trigonia* was recognized, and it is now in need of modern revision. This is all the more desirable given the major changes in trigonioid classification and nomenclature over the past 20 years.

The South African Museum holds large collections of trigonias from this formation. These include the material described by Kitchin (1908), the early Geological Survey collections, and subsequent collections made by the late E. C. N. van Hoepen and the writer. There are also small collections in the Port Elizabeth Museum, the Albany Museum, and the University of Zimbabwe, which the writer has studied.

The repositories of material cited herein are as follows:

AM = Albany Museum, Grahamstown
PEM = Port Elizabeth Museum, Port Elizabeth
SAM = South African Museum, Cape Town.

GEOLOGY

The Cretaceous deposits of the Algoa Basin are assigned to the Uitenhage Group. At the base are fanglomerates and coarse fluviatile clastics of the Enon Formation. These grade vertically and laterally into finer clastics of the Kirkwood Formation, deposited by high-sinuosity streams in a marginally marine environment. A marine tongue of the Infanta Shale, known as the Colchester Member, is intercalated within the Kirkwood Formation and reflects earliest Cretaceous transgression. The occurrence of the Berriasian belemnite *Belemnopsis gladiator* Willey, in the Algoa Basin (Willey 1973; Cooper 1981) may serve to date this intercalation. The Sundays River Formation rests with toplap relationship and basin-margin disconformity on the Kirkwood. It is a strongly transgressive marine unit of richly fossiliferous mudstones, siltstones and fine-grained sandstones deposited in an intertidal to littoral situation (Shone 1976). The ammonite fauna, dominated by *Olcostephanus*, with occasional *Distoloceras*, *Neohoploceras*, *Partschiceras*, *Eodesmoceras*, *Bochianites* and *Umgazaniceras* (Cooper 1981, 1983), indicates a latest Valanginian age for surface exposures, though Hauterivian microfossils are reported from the subsurface (McLachlan & McMillan 1979).

SYSTEMATIC PALAEONTOLOGY

Order TRIGONIOIDA Dall, 1889

Discussion

If taxonomy is to reflect phylogeny, it is clear that the current subdivision of the Trigoniidae into as many as 19 subfamilies is inappropriate. It implies that this evolutionary radiation is devoid of phyletic lines and that no two subfamilies are more closely related to each other than to any other subfamily. This is spurious. On phylogenetic grounds these subfamilies are here distributed among two suborders and four superfamilies (Fig. 1).

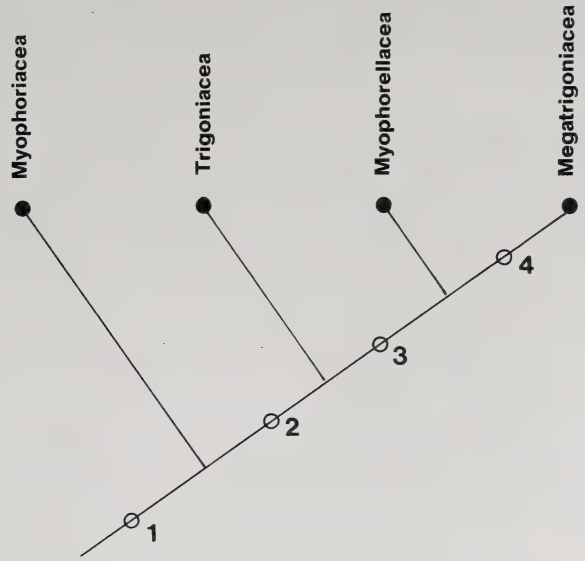

Fig. 1. Hypothesized relationships among the proposed superfamilies of Trigonioida. Character states: 1 = prominent marginal carina, myophorian hinge, radial ornament to area subordinate to transverse ornament; 2 = hinge trigonian, radial ornament to area predominant; 3 = marginal carina relatively fine, nodate, area with transverse ornament, flank costae predominantly nodate, mostly oblique or V-shaped; 4 = escutcheon carina generally obsolete and marginal carina commonly restricted to umbonal region, shell often pyriform or posteriorly rostrate, also somewhat produced and often inflated anteriorly.

Suborder TRIGONIINA Dall, 1889

Discussion

Since strict application of the phylogenetic principles of Hennig (1966) leads to almost as many supraspecific taxa as there are species, the writer prefers a more utilitarian approach in which paraphyly is preferred to a burgeoning and unwieldy higher taxonomy. Consequently, the suborder Trigoniina is here held to comprise the superfamilies Myophoriacea and Trigoniacea.

Superfamily MYOPHORIACEA Bronn, 1849

(*nom. transl.* herein *ex* family Myophoriidae Bronn, 1849)

Diagnosis

Generally small to medium-sized trigonioids with prosogyrous beaks, rarely orthogyrous or opisthogyrous. Dentition myophorian or schizodian, with smooth or weakly ribbed teeth. Main tooth of left valve opithsocline, simple or bilobed; two main teeth of right valve asymmetrical, posterior one generally longer and narrower. Additional teeth may be present in left valve, on one or both sides of main tooth, whereas additional relatively weak teeth may also be present anteriorly in right valve. Myophorous buttress generally weak or absent; pallial line distinct, mostly entire. Area not usually discriminated ornamentally from flank. Age: Upper Silurian–Triassic.

Discussion

Although Myophoriacea are absent from the present fauna, they are discussed because of their relevance to the revised classification presented here. The superfamily comprises the following taxa: Schizodidae (Schizodinae and Eoschizodinae), Scaphellinidae, Myophoriidae, Pachycardiidae (Pachycardiinae and Eoastartinae), and Minetrigoniidae (including Costatoriidae).

Superfamily TRIGONIACEA Lamarck, 1819

Diagnosis

Umbones orthogyrous to opisthogyrous, rarely prosogyrous; escutcheon usually present; bipartite area and flank differently ornamented in most genera; respiratory margin obliquely truncate or subtruncate; left valve with broad median tooth, strongly concave to deeply emarginate below in most genera; posterior left tooth marginal, weak or obscure; anterior left tooth moderately strong; right valve with two subequal, more-or-less symmetrically divergent teeth not borne on hinge plate; anterior marginal tooth very obscure in some species; main teeth with strong transverse ridges except in a few primitive forms; anterior myophorous buttress generally well developed.

Discussion

At present this superfamily comprises the families Gruenewaldiidae fam. nov., Trigoniidae (Pleurotrigoniinae and Trigoniinae), Neotrigoniidae (nom. transl. herein ex subfamily Neotrigoniinae Kobayashi) (Nototrigoniinae and Neotrigoniinae) and Prosogyrotrigoniidae (Praegoniinae and Prosogyrotrigoniinae) (Fig. 2).

The most primitive trigoniaceans are assigned to the family Gruenewaldiidae nov., in which the hinge is myophorian, with only partially striated teeth, and the areal ornament is predominantly transverse (Newell & Boyd 1975). At

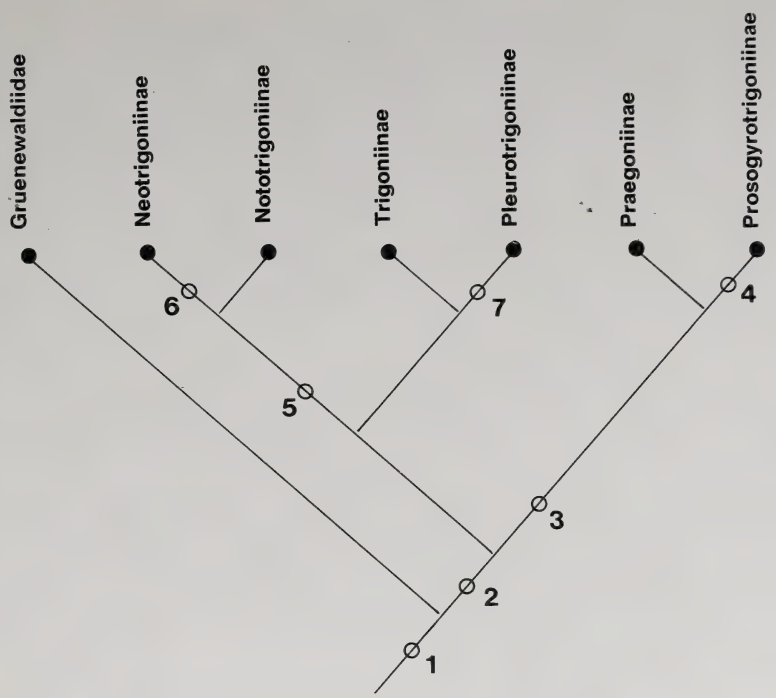

Fig. 2. Hypothesized relationships within the superfamily Trigoniacea. Character states: 1 = shell trigonal with prominent marginal carina and escutcheon, flank costae concentric, radial ornament to area subordinate to transverse ornament, hinge myophorian; 2 = hinge trigonian, area with radial ornament, at least in nepionic stages; 3 = shell ovate, marginal carina obsolete, beaks prosogyrous; 4 = area with concentric ornament; 5 = antecarinal sulcus very broad, shallow; 6 = area very broad, flanks wholly or partly with radial costae; 7 = marginal carina and ornament to area restricted to nepionic stages, flank costae terminate at anterolateral shoulder in prominent tubercles.

present only *Gruenewaldia* and *Lyriomyophoria* are assigned here and both are very small.

The trigonian hinge (Newell & Boyd 1975) first appeared in the mid-Triassic, derived from the gruenewaldiid condition. Almost immediately there was a fundamental dichotomy into the Trigoniidae and Prosogyrotrigoniidae. Whereas the latter taxon preserves the primitive condition of prosogyrous beaks, a predominantly transversely ornamented area (in all but *Praegonia*), and a weak hinge with the main tooth of the left valve ungrooved, the loss of the prominent marginal carina and the generally trigonally ovate to suborbicular shape, with rounded respiratory margin, are derived characters. The Trigoniidae, on the other hand, preserve the pronounced marginal carina of *Gruenewaldia* while accentuating the radial costation of the area. Their conspicuously striated main teeth and orthogyrous to opisthogyrous beaks are derived characters.

The Neotrigoniidae evolved from the Trigoniidae in the late Jurassic (Nakano 1970) by broadening and shallowing of the antecarinal sulcus. The

primitive subfamily Nototrigoniinae Skwarko, 1963 (including the Austrotrigoniinae Skwarko, 1968), is widely distributed in the Australasian Realm and is descended from *Opisthotrigonia*. The link between the Nototrigoniinae and Neotrigoniinae is provided by the late Cretaceous *Mesotrigonia* (Freneix 1958; Fleming 1964). Even should *Mesotrigonia* prove to be based upon juvenile *Pacitrigonia* (Nakano 1961), its ornament is sufficiently similar to that of *Eotrigonia* to support a phyletic relationship. Additional evidence is the predominantly Australasian distribution of both the Nototrigoniinae and the Neotrigoniinae. Darragh (1986) has recently suggested derivation of *Eotrigonia* from Neocomian species such as *Trigonia vertistriata* Skwarko and *T. marumbiana* Skwarko, via the late Cretaceous *T. miriana* Skwarko. The writer is unaware of any Senonian *Trigonia* s.s. and the long time gap between the last appearance of *Trigonia* (?Cenomanian) and the first appearance of *Eotrigonia* (Palaeocene) makes such a phylogeny untenable. *Trigonia miriana* differs substantially from all other *Trigonia* species in its small, inflated, quadrate shell with subterminal umbones, its steeply inclined, shallowly excavate escutcheon with faint radial costellae, its broad area that is wider than the flank, and in having pustulose flank costae that terminate posteriorly in a low node at the smooth antecarinal sulcus (Skwarko 1963). These differences warrant generic separation and *T. miriana* Skwarko is here designated type species of *Skwarkoella* gen. nov. It is believed to be a member of the Nototrigoniinae.

Contrary to Newell & Boyd (1975), the writer believes that radially ornamented Permo-Triassic forms such as *Costatoria*, *Procostatoria* and *Minetrigonia* are unrelated to *Neotrigonia*, and that the similarities are due to convergence. This is supported by the long time gap between the last appearance of Minetrigoniidae and the first appearance of Neotrigoniinae.

Family **Trigoniidae** Lamarck, 1819

Diagnosis

Trigonal to rhomboidal, very inequilateral trigoniaceans; dentition trigonian, with conspicuously striated main teeth; escutcheon prominent; broad area with obliquely truncate respiratory margin; posterodorsal margin straight; flank ornament nontuberculate, subconcentric; carinae prominent, generally persisting to maturity, with prominent antecarinal sulcus; area typically with radial ornament, but in some may become smooth in maturity.

Discussion

As restricted here, the family Trigoniidae comprises only the nominate subfamily and the Pleurotrigoniinae van Hoepen, 1929, in which the very narrow escutcheon is unornamented, the marginal carina becomes obsolete in maturity, the radial costellae to the area are restricted to the nepionic stages, and the flank costae bear a tubercle at the anterolateral shoulder.

Subfamily Trigoniinae Lamarck, 1819

Diagnosis

Small to moderately large trigoniids; umbones well developed; carinae and radial costellae to area persisting to maturity; marginal carina corded; antecarinal groove variable, often restricted to left valve.

Genus *Trigonia* Brugière, 1789

Type species. *Venus sulcata* Hermann, 1781; ICZN Opinion 327 (1955).

Diagnosis

Escutcheon with radial ornament; flank costae terminating at the antecarinal sulcus or marginal carina.

Discussion

Neuquenitrigonia Leanza & Garate (1987) has transverse costellae to the escutcheon, whereas *Guineana* Skwarko, 1967, has flank costae that continue on to the area to produce cancellate ornament. The Upper Triassic *Heslingtonia*, which is here elevated to generic status, differs from *Trigonia* in the effacement of costae from the posterior part of the flank, and in the fine radial sculpture of the area and narrow escutcheon (Fleming 1987). Given the vast number of *Trigonia* s.s. species now known, if taxonomy is to reflect phylogeny, current perceptions of the genus are too broad and this taxon requires further phylogenetic subdivision.

Trigonia tatei Neumayr, 1882

Fig. 3

Trigonia cassiope d'Orbigny. Tate, 1867: 158. Lycett, 1877: 172.
Trigonia tatei Neumayr (*in* Holub & Neumayr), 1881: 275, pl. 2 (fig. 3). Kitchin, 1908: 125. Lambert, 1944: 371.
non *Trigonia (Trigonia)* aff. *tatei* Neumayr. Rennie, 1947: 58, pl. 2 (figs 11–13) (= *Trigonia* sp.).

Type

By lectotype designation herein, the original of the specimen figured by Neumayr (*in* Holub & Neumayr 1881, pl. 2 (fig. 3)).

Material

A total of 22 specimens were examined: SAM–4646, D1876 (2 specimens), D1881–82, D1893 (9 specimens), D1896, D1932 and D1973 (2 specimens), as well as 4 unnumbered specimens also in the South African Museum collections.

Description

Shell medium sized (maximum length about 70 mm), trigonally ovate, elongate (H/L = 0,71–0,73), with moderately elevated umbones situated about

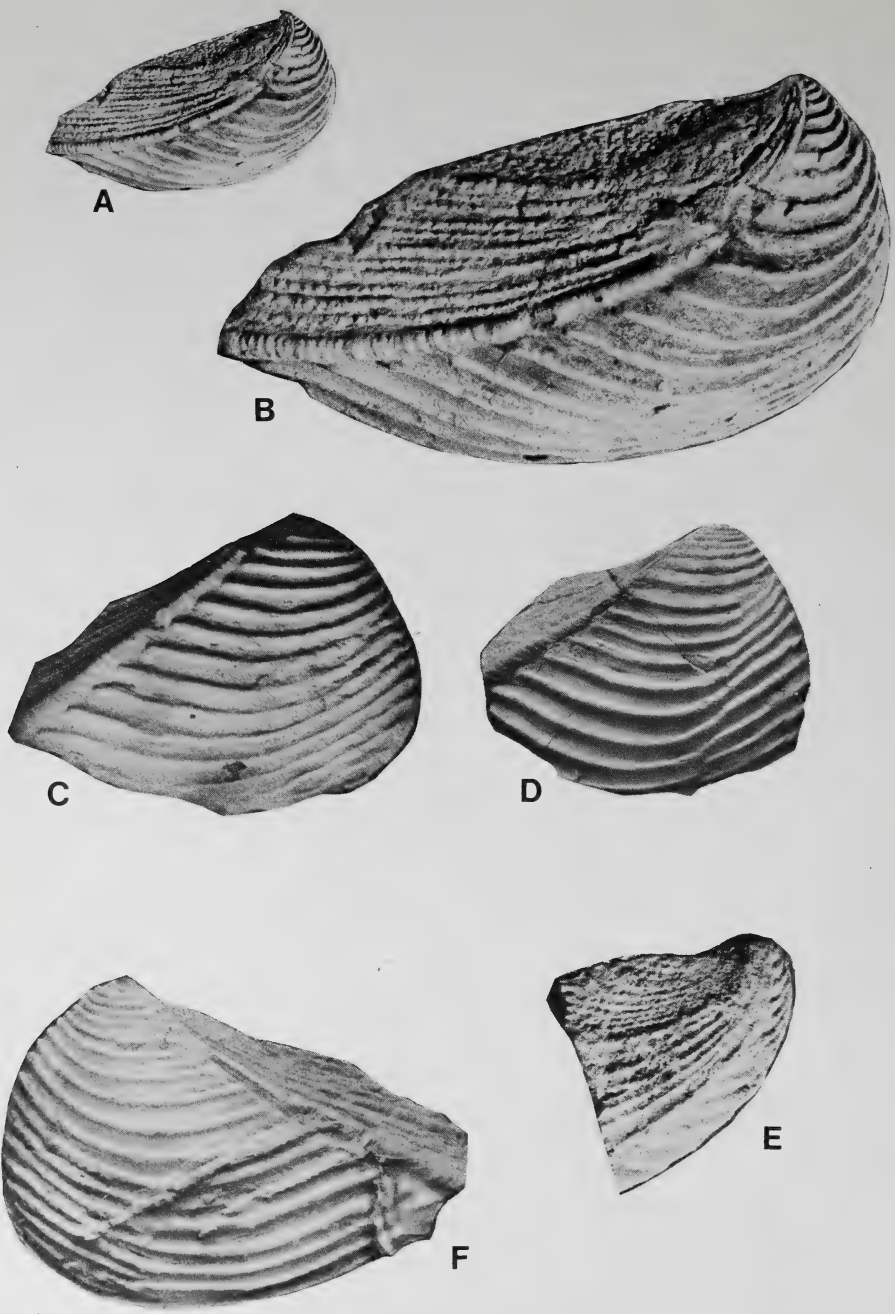

Fig. 3. *Trigonia tatei* (Sharpe). A–C. Dorsal (× 1 and × 2) and lateral views of an unnumbered right valve in the South African Museum. Note the absence of an antecarinal sulcus. D–E. SAM–D1876, a right valve. D. Lateral view showing obliquity and crowding of flank costae anteriorly. E. Dorsal view of umbonal region, × 2. Note the beaded radial costellae to the escutcheon which curve to meet the dorsal commissure. F. Lateral view of an unnumbered left valve in the South African Museum, × 1. Note the distinct antecarinal sulcus.

one-quarter of the shell length from the anterior and weakly inturned, opisthogyrous beaks. The valves are moderately weakly inflated (W/H = 0,28–0,33), with an almost straight posterodorsal margin at right angles to the broadly convex anterior margin. The ventral margin is broadly convex and the moderately short respiratory margin obliquely truncate.

The escutcheon is lanceolate, slightly more than half the shell length, and is ornamented with radial rows of fine tubercles that, on D1876, curve inward to meet the commissure. The trigonal area is relatively narrow and almost flat. It is ornamented by finely beaded radial costellae, one of which corresponds to the escutcheon carina. There is no median groove to the area. The marginal carina is marked by a prominent rib that thickens posteriorly and is crossed by growth lirae that give it a scaly corded appearance.

The flanks are ornamented with up to 28 pronounced, subconcentric costae that are slightly narrower than the interspaces on the posterior half of the shell. In maturity, the ribs flex slightly upwards anteriorly, becoming slightly oblique, crowded and broader than the interspaces. Posteriorly the ribs terminate against the marginal carina of the right valve, but there is a narrow antecarinal sulcus to the left.

Discussion

Rennie (1947) compared material from the Lower Aptian of southern Moçambique with this species, but it differs in being slightly more elongate, with a more convex anterior margin, and in having maximum downward convexity of the flank costae more anterior than in Uitenhage material. It probably represents a new species.

Occurrence

Trigonia tatei Neumayr is known with certainty only from the Upper Valanginian of south-east Africa, where it is an uncommon element of the faunas.

Suborder MYOPHORELLINA nov.

Discussion

This monophyletic suborder is here held to comprise the superfamilies Myophorellacea and Megatrigoniacea.

Superfamily MYOPHORELLACEA Kobayashi, 1954
(*nom. transl.* herein *ex* subfamily Myophorellinae Kobayashi, 1954)

Diagnosis

Small to very large trigonioids, suborbicular to ovate, trigonal and subquadrate; strongly inequilateral; posteriorly produced, with subterminal umbones; marginal and inner carinae prominently nodate, generally persisting to maturity;

area broad, typically with transverse ornament and longitudinal groove often marked by row of nodes; respiratory margin generally broadly truncate; escutcheon smooth, nodate, or with transverse ornament; flank ribs primitively subconcentric and entire but mostly strongly oblique and nodate, in derived forms may form chevrons.

Discussion

This superfamily comprises the families Frenguelliellidae (Frenguelliellinae and Laevitrigoniinae) with subconcentric, more or less entire, flank costation, Myophorellidae (Myophorellinae and Steinmanellinae subfam. nov.) with obliquely nodate flank costation, and the derived Vaugoniidae (Vaugoniinae and Quadratotrigoniinae) with nodate, V-shaped flank costae. The Frenguelliellinae (Fig. 4) preserve the primitive condition of subconcentric flank costae and

Fig. 4. Hypothesized relationships within the Myophorellacea. Character states: 1 = flank costae subconcentric, beaded inner and marginal carinae which persist to maturity, escutcheon smooth, area with fine transverse ornament; 2 = antecarinal sulcus virtually obsolete, nodose flank costae oblique, escutcheon sometimes with transverse costellae, longitudinal furrow to area often delimited by row of nodes; 3 = flank costae form chevrons near umbo; 4 = large, massive, carinae breaking up into rows of nodes or becoming obsolete in maturity, area often with transverse growth rugae in maturity; 5 = large, massive, carinae replaced by prominent nodes, longitudinal furrow delimited by prominent nodes, escutcheon with radial rows of nodes, area with transverse growth rugae in maturity, comprises *Quadratotrigonia* homoeomorphs; 6 = shell ovate, very broad antecarinal sulcus shallow and unornamented, weak irregular flank costae commonly pustulose or with oblique rows of pustules.

prominent antecarinal sulcus, linking it to ancestral trigoniaceans, but have the myophorelline synapomorphies of nodate marginal and escutcheon carinae, smooth escutcheon and transversely ornamented area, whereas the ribs in some, e.g. *Jaworskiella*, show a tendency to become nodate. The Laevitrigoniinae Saveliev, 1958, are frenguellielline descendants in which the subconcentric flank costation is irregularly nodate and the antecarinal sulcus is very wide and shallow. The Myophorellinae are frenguelliellid descendants in which the flank costae are oblique in maturity and ornamented with conspicuous nodes. *Jaworskiella* is an intermediate stage. The Steinmanellinae subfam. nov. are myophorelline descendants that evolved in parallel with the Quadratotrigoniinae. The latter are derived from Vaugoniinae that evolved from Myophorellinae by the development of V-shaped flank costae in the early and middle growth stages.

Family **Myophorellidae** Kobayashi, 1954

(*nom. transl.* herein *ex* subfamily Myophorellinae Kobayashi, 1954)

Diagnosis

Myophorellaceans with generally conspicuously nodate flank costae that are subconcentric near the umbo, commonly becoming strongly oblique in maturity.

Subfamily Myophorellinae Kobayashi, 1954

Diagnosis

Small to moderately large myophorellids; trigonally ovate to suborbicular; escutcheon smooth or transversely ornamented; area with fine transverse costellae; costae oblique over much of flank, often discontinuous anteroventrally or joined by intercalatories.

Discussion

Morphologically the most primitive myophorelline is *Ibotrigonia* Kobayashi (*in* Kobayashi & Tamura, 1957), which preserves subconcentric flank costae that are broken up unevenly into tubercles, and with an irregularly serrated marginal carina. Although it has been included (Poulton 1979) in the synonymy of *Myophorella*, Cox (1969) and Hirsch (1980) are followed in regarding it a valid taxon.

Pseudomyophorella Nakano, 1961, stands in the same relationship to *Myophorella* as *Paranditrigonia* does to *Anditrigonia* and *Arabitrigonia* to *Scabrotrigonia*. It is here considered a valid genus within the Myophorellinae characterized by radial costellae to the area. *Scaphotrigonia* Dietrich, 1933, is a widely recognized genus within the Myophorellinae, characterized by its nearly straight flank costae, enlarged nodes to the anterolateral shoulder, and short subhorizontal costae to the flat anterior face.

Genus *Myophorella* Bayle, 1878

Type species. *Trigonia nodulosa* Bayle (= *T. nodulosa* Lamarck, 1801); by the subsequent designation of Crickmay (1932).

Diagnosis

Escutcheon smooth; area relatively broad, with or without nodes demarcating the longitudinal furrow; marginal carina persisting to maturity; flank costae evenly curved, nodes predominating, without greatly enlarged nodes or intercalatories anteriorly.

Discussion

Within *Myophorella* it is possible to recognize several subgenera:
M. (Myophorella)—escutcheon smooth; flank costae distinctly curved, essentially uninterrupted, with prominent nodes.
M. (Promyophorella)—like *Myophorella*, but with ribbing dominant and fine tuberculation.
M. (Scaphogonia)—like *Promyophorella*, but with a vertical row of enlarged nodes on the anterolateral shoulder and anterior ribs that are separated by a gap from the flank ribs; apparently endemic to North America.
M. (Clavotrigonia)—like *Myophorella* but relatively large, subtrigonal; anterior face almost straight, with subangular anteroventral margin; flank costae distant, weakly curved, not crowded dorsally, meeting the marginal carina almost at right angles, or with a very short, strongly upcurved taper; a predominantly Tethyan subgenus.

Although *Scaphogonia* was treated as a strict synonym of *Myophorella* by Cox (1969) and Poulton (1979), the latter worker observed that its diagnostic characters serve '. . . to distinguish these (North American) species from nearly all otherwise similar Middle and Late Jurassic European *Myophorella* species' (p. 27). On this basis *Scaphogonia* is retained as a valid subgenus of *Myophorella*, apparently endemic to North America. Similarly, there are a host of European *Myophorella* species that are closer to the type of *Clavotrigonia* (of which *Clavitrigonia* Leanza, 1942, is a junior objective synonym) than they are to the type of *Myophorella* s.s. The subgenus *M. (Clavotrigonia)* is here applied to this predominantly Tethyan group.

Although *Haidaia* Crickmay, 1930, has been rejected (Cox 1952, 1969; Poulton 1979) as a junior objective synonym of *Myophorella*, it was regarded as subgenerically distinct by Leanza (1981) and Leanza & Garate (1987). The type species, *M. dawsoni* (Whiteaves) was redescribed by Poulton (1979: 33, pl. 1 (figs 12–21), pl. 2 (figs 1–4)) and the writer concurs that its features are essentially those of *Myophorella* s.s.

The taxonomic position of the mid-Jurassic *Awadia* Hirsch, 1980, is currently uncertain. It is assumed to be a myophorellacean that, in its broad, radial, nontuberculate flank costae and smooth area, is convergent toward the Pterotrigoniinae.

There are, however, still many species of *Myophorella* that do not fit comfortably into any of the above taxa (cf. Leanza & Garate 1987) and the species to be described below is one of these. Until a major phylogenetic study of the Myophorellinae is undertaken, the writer hesitates to apply a new subgeneric name to the present species.

Myophorella first appeared in the Lias and attained a cosmopolitan distribution in the later Jurassic, becoming extinct in the Hauterivian.

Myophorella oosthuizeni Cooper, 1979

Fig. 5

Myophorella (Myophorella) oosthuizeni Cooper, 1979*a*: 22, fig. 1.

Types

The holotype, SAM–PCU5941 (RO–300), together with four paratypes, all of which are in the South African Museum, Cape Town, as well as SAM–D1875 (2 specimens).

Description

Shell small (maximum length about 60 mm), trigonally ovate, longer than high (H/L = 0,79), moderately inflated (W/H = 0,42), and somewhat produced posteriorly. Umbones subterminal, elevated, with moderately inturned, opisthogyrous beaks. Posterodorsal margin shallowly concave, anterior and ventral margins broadly rounded forming a semi-circle, respiratory margin obliquely truncate.

The sunken escutcheon is large, lanceolate, smooth, and extends almost the entire posterodorsal length of the shell. The marginal and escutcheon carinae are marked by rows of large, regular, obliquely clavate tubercles that increase in size posteriorly; those of the escutcheon carina are elongated anteromedially and those of the marginal carina posteromedially. Each tubercle of the marginal carina corresponds with a flank costa. The area is trigonal, rather narrow and ornamented with uniform, fine, transverse costellae that show no sign of strengthening posteriorly. There is a well-developed longitudinal groove that is situated close to the escutcheon carina.

The flank ornament of the nepionic stages comprises subconcentric ribs that pass with an inflexion across the marginal carina on to the area. The remaining flank costae are strongly oblique, posteriorly meeting the marginal carina at an angle of *c.* 30°. Except for the posterior few ribs, most flank costae curve strongly forwards to meet the anterior and anteroventral commissures almost at right angles. All flank costae bear rather sharp, pointed tubercles and nodes that, on the anterior part of the valve, are concentrically elongated. There is a gap in some of the ribs terminating along the anteroventral margin, with some irregularity of tuberculation, in *Scaphotrigonia* fashion. The entire flank surface is ornamented with conspicuous growth lirae that are continuous with the costellae of the area.

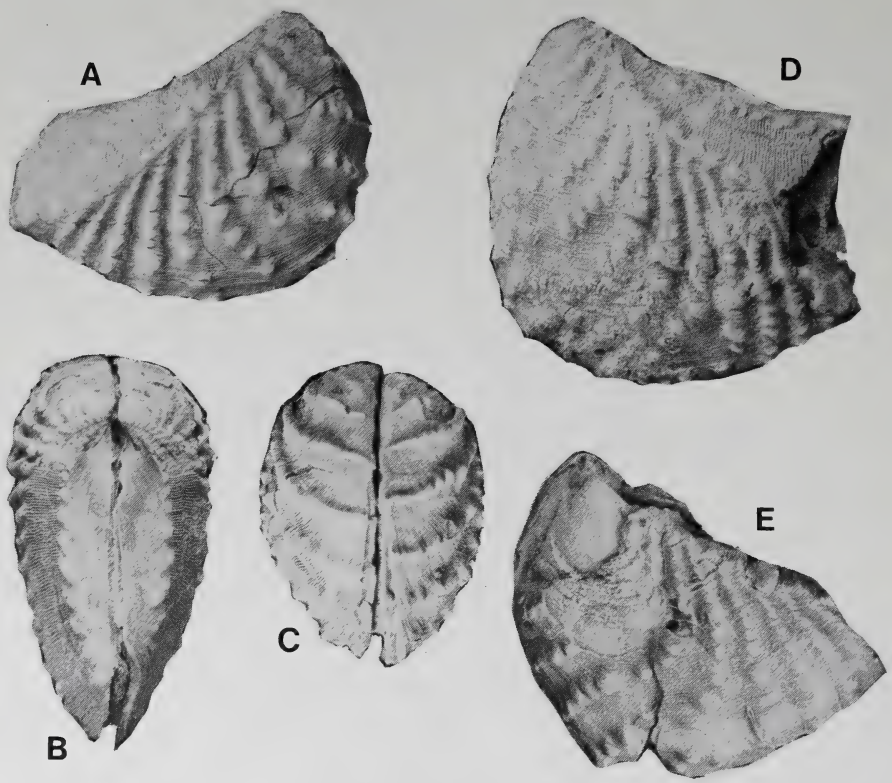

Fig. 5. *Myophorella oosthuizeni* Cooper, × 1. A–C. Lateral, dorsal and anterior views of the holotype, SAM–PCU5941. D. Left valve of a paratype in the South African Museum. E. Left valve of a paratype in the South African Museum.

Occurrence

Myophorella oosthuizeni Cooper is known only from the Upper Valanginian of south-east Africa, where it is a very rare element of the faunas.

Subfamily Steinmanellinae subfam. nov.

Diagnosis

Generally very large, massive, trigonally ovate to quadrate and elliptical myophorellids; escutcheon narrow, lanceolate, with irregular, radially elongated tubercles; median groove to area marked by rows of coarse nodes; area of early and middle growth stages with transverse growth striae, later remaining smooth or with coarse, irregular growth rugae, which may extend on to the flanks; flank costae tend to become crowded ventrally, where they may bend sharply forwards and coalesce to form irregular concentric growth rugae.

Discussion

Poulton (1977, 1979) included *Steinmanella* in the synonymy of *Myophorella* but such treatment cannot be justified morphologically or phyletically. As here interpreted, the Steinmanellinae arose from a myophorelline ancestor late in the Jurassic by an increase in size, with the shell becoming massive and robust, losing its delicate gracile character. The longitudinal groove to the area is marked by a row of conspicuous nodes, of similar strength to those forming the marginal and escutcheon carinae, whereas the transverse growth striae of the area are replaced in maturity by coarse, irregular growth rugae. The earliest genus in the subfamily is *Steinmanella* itself, which first occurs in Tithonian rocks of South America (Leanza & Garate 1987). Simply by failure to produce coarse irregular growth rugae across the mature area, *Steinmanella* gave rise to *Yaadia*, a predominantly North Pacific genus (Saul 1979). The latter lineage persisted into the Upper Cretaceous with the replacement of *Yaadia* by its subgenera *Yeharella* and *Setotrigonia*, both of which have been interpreted previously (Cox 1969) as subgenera of *Steinmanella*. Although Saul (1979), Tashiro (1988) and Tashiro & Kano (1989) included *Yeharella* within the strict synonymy of *Yaadia*, it seems to be phyletically important and is here retained at the subgeneric level. Significantly, Tashiro & Kano (1989, fig. 4) showed the Japanese species of *Yaadia* as having evolved in parallel with their North American counterparts. *Yeharella* differs from ancestral *Yaadia* in the early effacement of the radial rows of nodes from the area, leaving the latter smooth for most of its ontogenetic development. In addition, the flank costae of *Yeharella* are not interrupted anteroventrally or accompanied by enlarged tubercles at the anterolateral shoulder (Saul 1979). *Setotrigonia* was said to differ from *Yaadia (Yeharella)* in that the flank costae are broken into segments of various lengths and continue on to the area as narrow, wavy, transverse ridges (Cox 1969). Tashiro & Morozumi (1982) questionably included it in the synonymy of *Yaadia*. As here envisaged, the Steinmanellinae comprise *Steinmanella*, *Yaadia* s.s. and *Y. (Yeharella)*. The suprageneric placement of *Mediterraneotrigonia* Nakano, 1974*a*, is uncertain.

The morphologically similar Quadratotrigoniinae are a convergent, predominantly Tethyan group; they are phyletically distinct and can be distinguished from the Steinmanellinae nov. by the V-shaped costae of the umbonal region and their conspicuously ornamented areas (Nakano 1968).

Genus *Steinmanella* Crickmay, 1930

Type species. *Trigonia holubi* Kitchin, 1908; by original designation.

Diagnosis

Steinmanellines in which the escutcheon is ornamented with radial rows of irregular nodes, which may be continuous with the coarse growth rugae of the posterior part of the area; flank costae generally weakly curved, uninterrupted, and coarsely nodate. Age: Tithonian–Neocomian.

Steinmanella holubi (Kitchin, 1908)

Figs 6–8

Trigonia sp. 2 Sharpe, 1856: 202.
Trigonia holubi Kitchin, 1908: 103, pl. 4 (fig. 2). Stoyanow, 1949: 68.
Steinmanella holubi (Kitchin) Crickmay, 1930: 50. 1932: 458. Cox, 1969: N487, fig. D74.6. Levy, 1969: 66. Cooper, 1979*b*: 63, fig. 12. Saul, 1979: 6, fig. 2.
Steinmannella holubi (Kitchin) Kobayashi & Amano, 1955: 195.
Trigonia (Steinmanella) holubi Kitchin. Rennie, 1936: 346.
Yaadia holubi (Kitchin) Cox, 1952: 57. Pringle, 1960: 89.
Myophorella (Steinmanella) holubi (Kitchin) Poulton, 1977: 9.
Steinmanella cf. *holubi* (Kitchin) Cooper, 1983: 63.

Type

By lectotype designation of Rennie (1936: 350), the original of the specimen figured by Kitchin (1908, pl. 4 (fig. 2)), SAM–PCU3981 (Fig. 6).

Material

A total of 59 specimens were available for study in the South African Museum; SAM–D1881 (25 specimens), D1977 (3 specimens), D1979, D1989, D2541, and 28 without catalogue number.

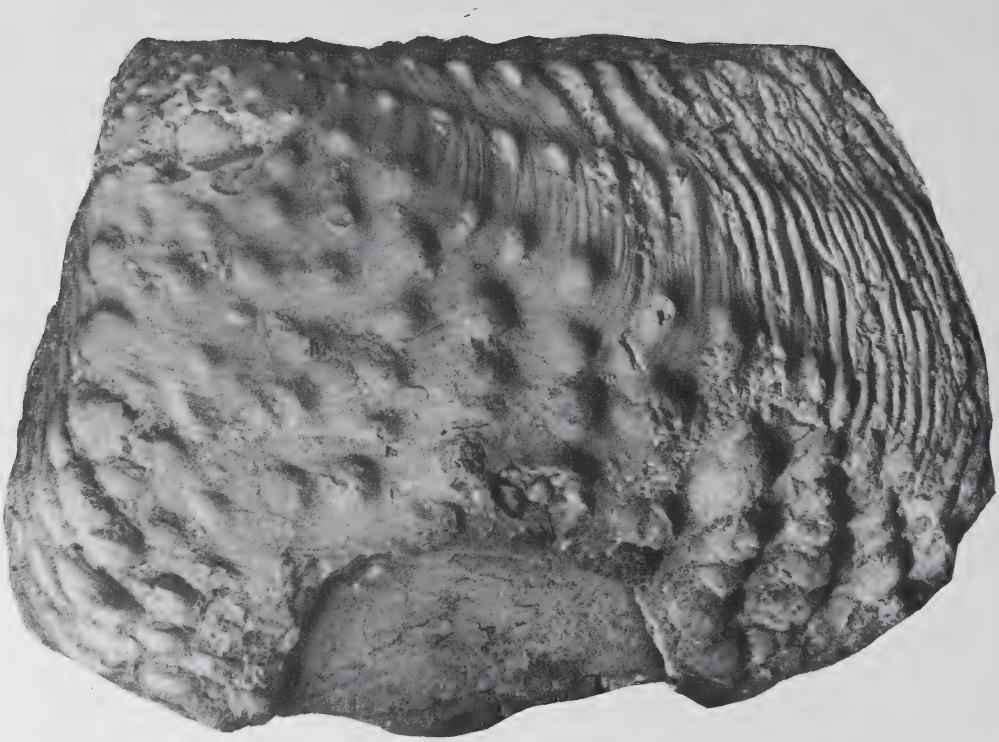

Fig. 6. *Steinmanella holubi* (Kitchin), × 1. The lectotype, SAM–PCU3981, in lateral view.

Fig. 7. *Steinmanella holubi* (Kitchin), × 1. Lateral view of an unnumbered topotype in the South African Museum.

Description

The shell is large (maximum length 128 mm), massive, quadrate, somewhat longer than high (H/L = 0,59–0,78), with inconspicuous terminal umbones and an abruptly truncate anterior face. The dorsal and anterior margins are straight, the ventral margin broadly rounded, and the broad respiratory margin subtruncate. The valves are weakly inflated (W/H = 0,27–0,34) and the inturned beaks orthogyrous to slightly opisthogyrous.

The escutcheon is very narrow, lanceolate, and ornamented with irregular rows of bullae that follow the growth lines and are continuous with the growth rugae of the area. There is a narrow lunule, about one-third of the shell height. The ligament pit is well developed, lanceolate, and may extend 40–50 per cent of the length of the escutcheon. The positions of the escutcheon and marginal carinae are marked by rows of prominent nodes, as is the dorsal edge of the longitudinal groove to the area. In maturity the tubercles of the escutcheon and marginal carinae are drawn out and eventually coalesce to produce irregular transverse ridges that parallel the growth lines. The longitudinal groove to the area persists to maturity, and is closer to the escutcheon than the flank. The broad trigonal area is essentially flat; in the nepionic stages it is crossed by subconcentric flank costae but in the middle growth stages is ornamented only by

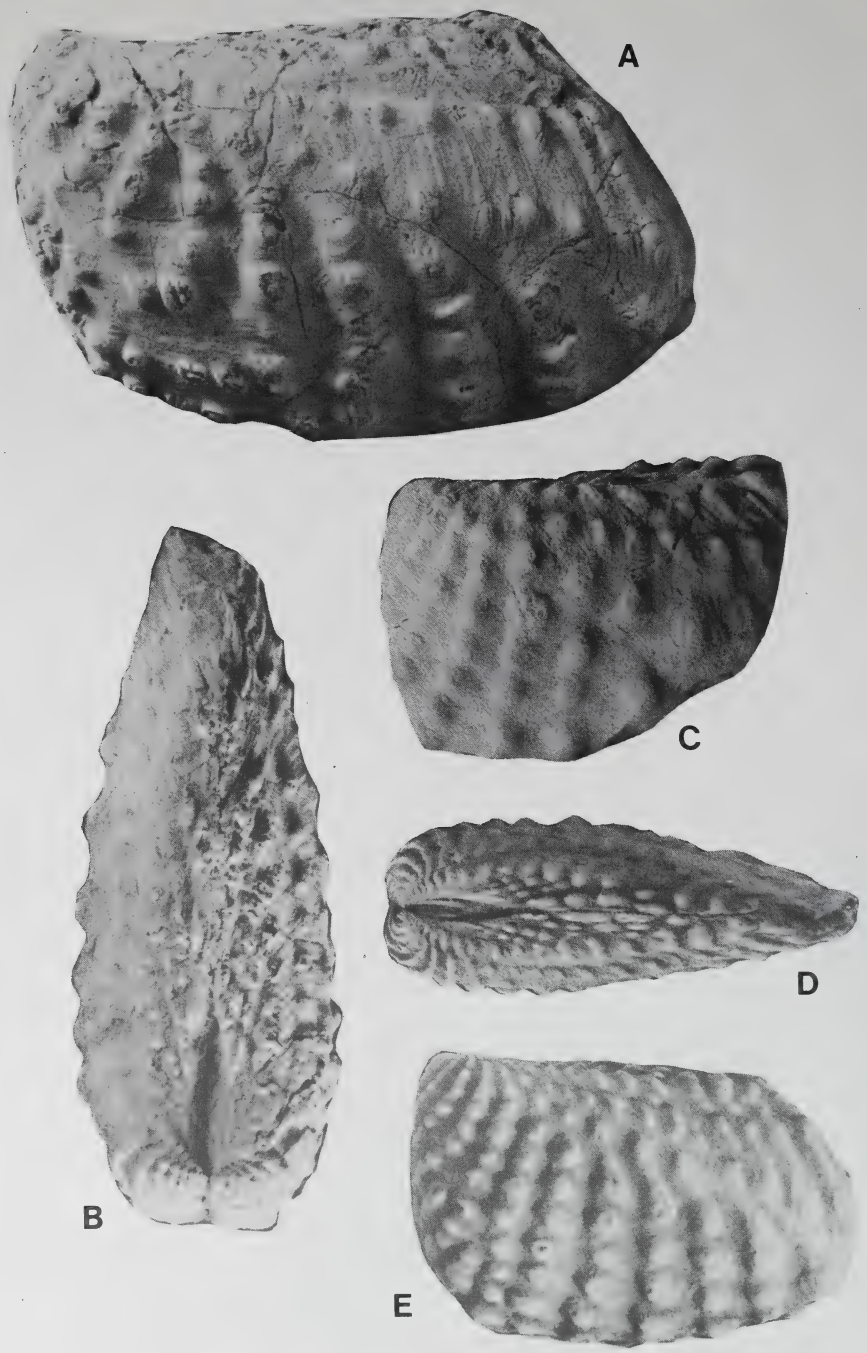

Fig. 8. *Steinmanella holubi* (Kitchin), × 1. A–B. Lateral and dorsal views of an aberrant individual in which the flank costae are interrupted anteroventrally. C. Lateral view of a fragmentary left valve from the Mngazana Formation of Transkei, in the South African Museum. D–E. Dorsal and lateral views of a juvenile, PEM–1208c.

growth striae and the median row of tubercles. These are replaced by irregular, transverse growth rugae in maturity.

Flank ornament comprises *c.* 16 distant rows of prominent nodes that curve slightly to the anterior, the nodes becoming more crowded ventrally with an occasional intercalated row along the anteroventral margin. The interspaces are slightly narrower than the rows of nodes. Along the ventral margin of mature shells, the tubercles tend to become elongated and may coalesce to form concentric growth rugae. In many individuals, the distal terminations of the ribs curve strongly to the anterior. Ornamentation does not extend on to the flattened anterior face and the latter is ornamented only by deep grooves and ridges parallel to the growth striae.

Occurrence

Steinmanella holubi (Kitchin) is endemic to the Upper Valanginian of south-east Africa. It abounds in the more argillaceous units of the Sundays River Formation and also occurs in the Mngazana Formation of Transkei (Cooper 1983).

Steinmanella herzogi (Goldfuss, 1837)

Figs 9–12

Lyrodon herzogii (Hausmann MS) Goldfuss, 1837: 193, pl. 137 (fig. 5). Krauss, 1850: 453, pl. 48 (fig. 3).
Trigonia herzogi (Goldfuss) Steinmann, 1882: 220, pl. 7 (figs 1–2), pl. 9 (figs 1–2). Paulcke, 1903: 309. Kitchin, 1903: 102; 1908: 8, pl. 5 (fig. 1). Hatch & Corstorphine, 1905: 245, fig. 66 (left-hand side). Stoyanow, 1949: 68. Levy, 1969: 66.
Trigonia (Steinmanella) herzogi (Goldfuss) Rennie, 1936: 346.
Steinmannella herzogi (Goldfuss) Kobayashi & Amano, 1955: 195. Reyes *et al.*, 1981: 35, pl. 1 (fig. 13).
Yaadia herzogi (Goldfuss) Pringle, 1960: 89.
?Steinmannella (Steinmannella) herzogi (Hausmann) Reyes, 1970: 15, pl. 3 (fig. 2), pl. 4 (figs 1–3).
Steinmanella herzogi (Goldfuss) Cooper, 1979*b*: 63.

Type

The whereabouts of Goldfuss' (1837) type material is unknown; it may prove necessary to designate a neotype.

Material

In addition to 106 specimens in the South African Museum, SAM–4416, 4994, 5035–36, 7498, 7520, D164, D1840, D1881, D1892 (13 specimens), D1911 (40 specimens), D1914, D1916, D1940 (3 specimens), D2541 and 41 specimens without number, PEM–1463/52–3 and AM–2428 were also available for study.

Description

Shell very large (maximum length 150 mm), massive, posteriorly very elongate (H/L = 0,52–0,63), with moderately inflated valves (W/H =

Fig. 9. *Steinmanella herzogi* (Goldfuss), × 1. Lateral view of the provisional neotype, SAM–PCU4416.

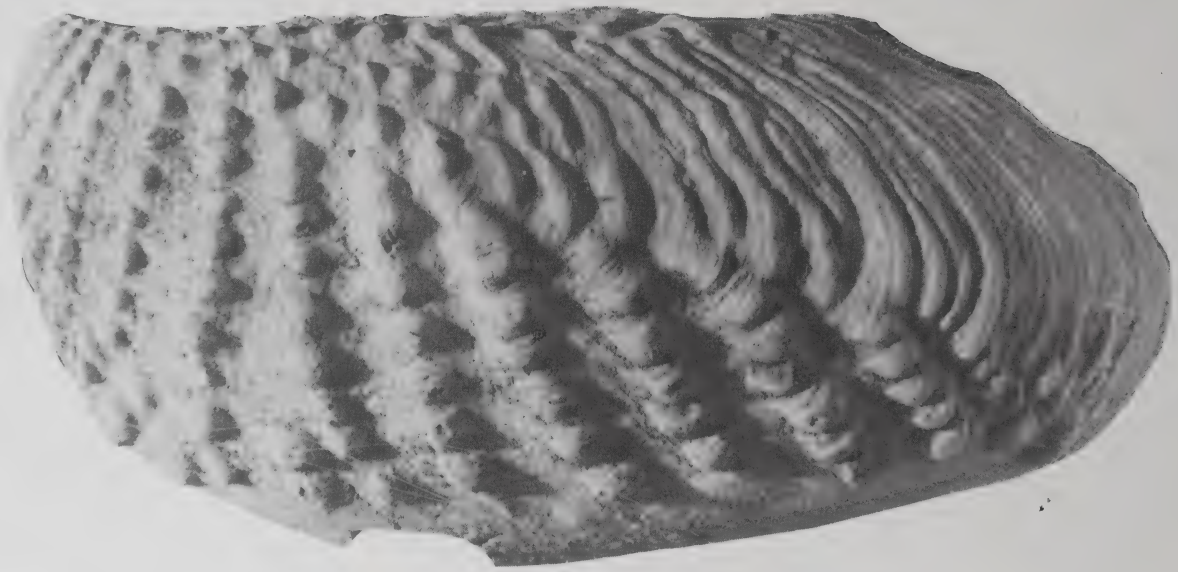

Fig. 10. *Steinmanella herzogi* (Goldfuss), × 0,9. Lateral view of PEM–1463/52.

Fig. 11. *Steinmanella herzogi* (Goldfuss), × 1. A–B. Lateral and dorsal views of a specimen in the Port Elizabeth Museum. C. Lateral view PEM–1463/53.

Fig. 12. *Steinmanella herzogi* (Goldfuss), × 1. Lateral, dorsal and anterior views of AM–2428 in which the tubercles are diagonally elongate. Note the lack of tubercles to the anterior face.

0,29–0,36). The straight dorsal and weakly curved anterior margins form an acute angle, with terminal umbones and weakly inturned, orthogyrous to slightly opisthogyrous beaks. The ventral margin is very long, weakly convex, and the broad respiratory margin subtruncate.

The escutcheon is fairly narrow, and about two-thirds the length of the shell. It is ornamented by irregular oblique rows of elongate tubercles that vary in size and follow the growth striae. Posteriorly these tubercles are continuous with the growth rugae of the area. There is a very narrow lunule, about 40 per cent of the shell height. The ligament pit is moderately developed, lanceolate, and about 40 per cent of the length of the escutcheon. There are three rows of tubercles to the area, corresponding to the escutcheon and marginal carinae and the dorsal margin of the longitudinal groove. The number of tubercles in the marginal row approximates the number of flank costae. At lengths of 50–100 mm the tubercles of the area become elongated transversely to form coarse, irregular, growth rugae. The concentric flank costae of the nepionic stages pass on to the area, whereas the longitudinal furrow persists almost to maturity and is situated closer to the escutcheon than the flank.

The flanks are ornamented with coarse nodes that form almost straight rows directed posteroventrally over much of the shell surface. Anteriorly the tubercle rows are narrower than the interspaces but posteriorly they are as wide as, or slightly wider than, the interspaces. There may be some irregularity in the tubercle rows anteroventrally, with a few tubercles intercalated between rows.

Occurrence

Steinmanella herzogi (Goldfuss) is abundant in the Upper Valanginian of the Algoa Basin. It may also occur in the early Hauterivian of southern Chile.

Superfamily MEGATRIGONIACEA van Hoepen, 1929

(*nom. transl.* herein *ex* subfamily Megatrigoniinae van Hoepen, 1929)

Diagnosis

Small to very large myophorellines, commonly pyriform to very produced and rostrate posteriorly, frequently strongly inflated anteriorly; carinae obsolete, or entire and restricted to umbonal region; antecarinal sulcus lacking; area narrow, bipartite, with ridge marking longitudinal groove internally; area commonly smooth but in some with transverse, oblique or radial ornament; flanks variably ornamented, with subconcentric, V-shaped or strongly oblique costae, which may be entire, weakly nodate or strongly tuberculate; posteroventral shell margin generally crenulated internally.

Discussion

As here interpreted, the superfamily Megatrigoniacea comprises the families Megatrigoniidae (Megatrigoniinae, Apiotrigoniinae and Pterotrigoniinae), Rutitrigoniidae and Iotrigoniidae (Fig. 13).

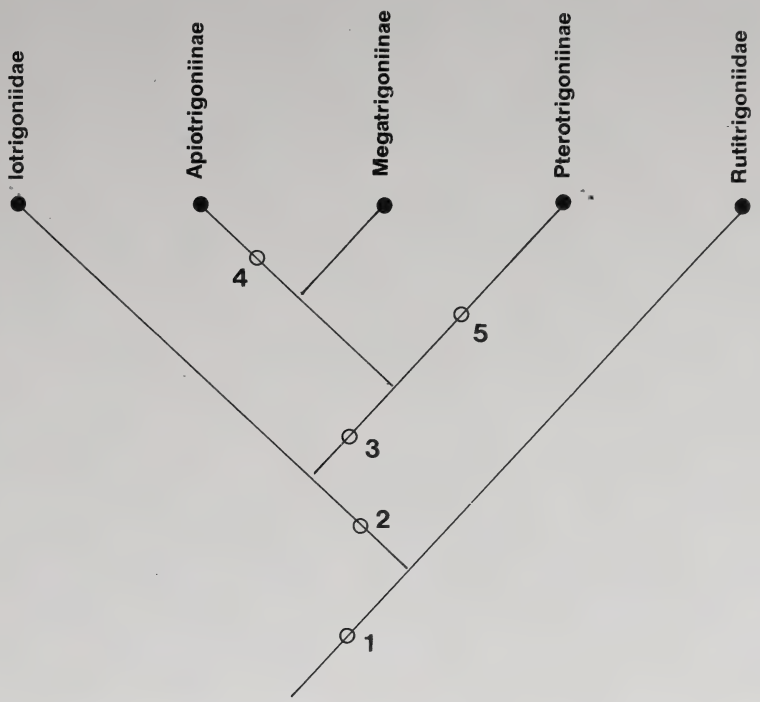

Fig. 13. Hypothesized relationships within the Megatrigoniacea. Character states: 1 = escutcheon carina obsolete or restricted to nepionic stages, marginal carina often restricted to umbonal region, anteriorly produced so that umbones are generally not subterminal, area relatively narrow with concentric ornament in nepionic stages later smooth, flank costae subconcentric; 2 = beyond nepionic stages flank costae V-shaped, with tendency to form nodes at anterolateral shoulder; 3 = posterior part of flank with straight, steeply inclined, finely crenulated and often crowded costellae, inner margin of shell crenulated posteroventrally; 4 = escutcheon with transverse costellae; 5 = posteriorly produced to rostrate, often inflated anteriorly, in some with subterminal umbones, flank costae strongly oblique varying from finely crenulated to spinose, respiratory margin generally rounded, escutcheon with transverse costellae.

Family **Megatrigoniidae** van Hoepen, 1929

(*nom. transl.* herein *ex* subfamily Megatrigoniinae van Hoepen, 1929)

Diagnosis

Commonly pyriform to subovate megatrigoniaceans that are generally weakly inflated anteriorly; carinae lacking or generally restricted to the nepionic stages; escutcheon smooth or with transverse costellae; area smooth or with transverse or radial costellae; flank costae V-shaped or oblique, weakly nodate, entire or tuberculate.

Discussion

As interpreted here, the family comprises the nominate subfamily, the Pterotrigoniinae van Hoepen, 1929, and the Apiotrigoniinae Tashiro, 1979.

Anditrigonia is the earliest megatrigoniine (Levy 1967*b*; Reyes & Pérez 1982); its diversity and abundance in South America leaves little doubt as to its Gondwanic origin. *Megatrigonia* is descended from *Anditrigonia* by a straightening of the flank costae from V-shaped to strongly oblique. Although *Columbitrigonia* Poulton, 1977, can be assigned to the Megatrigoniidae without difficulty, its subfamilial placement is more problematical. It was placed in the Megatrigoniinae by Poulton (1977) and the Apiotrigoniinae by Tashiro (1979). Contrary to Tashiro (1979), however, it lacks the fundamental apiotrigoniine characters of relatively small size, weak inflation, V-shaped flank costae and transversely costellate escutcheon. On the other hand, *Columbitrigonia* is strongly reminiscent of *Megatrigonia* in its large, robust shell, oblique flank costae, and smooth escutcheon, while resembling Pterotrigoniinae in its strong anterior inflation and posteriorly rostrate valves. Until its phylogeny is better understood, Poulton (1977) is followed in assigning it to the Megatrigoniinae.

Heterotrigonia and its allies are included in the Apiotrigoniinae by Tashiro (1979), but from virtually the first appearance of the subfamily there are two distinct phyletic lines (cf. Tashiro 1979, figs 17–18). Skwarko (1970), Nakano (1971) and Tashiro (1979) consider *Trigonia calderoni* Castillo & Aguilerae from the Oxfordian–Tithonian of New Mexico and Arizona (Stoyanow 1949; Reyes & Pérez 1982) to be the earliest apiotrigoniine. Whereas Skwarko (1970) and Tashiro (1979) referred this species to *Apiotrigonia*, Nakano (1971) assigned it to *Heterotrigonia*, Reyes & Pérez (1982) questionably included it in *Anditrigonia*, and Pérez & Reyes (1983) placed it in *Anditrigonia (Paranditrigonia)*. Given the smooth escutcheon and fine radial costellae to the area of *T. calderoni*, the latter assignment is followed here. *Anditrigonia (Paranditrigonia) calderoni* is thus the common ancestor to two phyletic lines that persisted until the close of the Cretaceous (Tashiro 1979). Since treatment of *Paranditrigonia* as a subgenus of *Anditrigonia* emphasizes primitive characters, when it is the derived characters (radial ornament to the area) that are phyletically important, *Paranditrigonia* is elevated to generic status and included as the most primitive representative of the Heterotrigoniini new tribe. As such, the subfamily Apiotrigoniinae is divided into the nominate tribe Apiotrigoniini (comprising *Apiotrigonia*, *Dampietrigonia*, *Turkestanella* and *Microtrigonia*) and the tribe Heterotrigoniini nov. (with *Paranditrigonia*, *Heterotrigonia* and *Nakanotrigonia*).

The origins of the Pterotrigoniinae are more cryptic. The subfamily first appeared in the Lower Tithonian of India (Spath 1935; Kobayashi & Amano 1955; Cox 1961) and rose to dominance in the Cretaceous. Although widely interpreted as descended from the Myophorellinae (Kobayashi & Nakano 1957; Nakano & Numano 1961; Nakano 1974*a*; Tashiro & Matsuda 1986), this view is based upon a comparison with relatively derived members of the Pterotrigoniinae, viz. *Pterotrigonia* and *Ptilotrigonia*, when it is the characters of the most primitive representatives, i.e. *Pisotrigonia*, that must carry the most weight phylogenetically. Some individuals of *Megatrigonia* (cf. Figs 15B, 16B) closely approach the *Pisotrigonia* condition, differing mainly in being larger, less-

inflated anteriorly and pyriform in outline, with a strongly convex anterior margin.

Subfamily Megatrigoniinae van Hoepen, 1929

Diagnosis

Shell generally large, massive, pyriform; respiratory margin rounded and anterior margin convex; escutcheon carina lacking, marginal carina restricted to nepionic stages; bipartite area initially with concentric ribs, later smooth; flank costae primitively subconcentric anteriorly and subvertical and crowded posteriorly, hence V-shaped; later strongly oblique anteriorly and weakly nodate.

Discussion

Megatrigonia is known with certainty only from Tithonian and Neocomian rocks of the east coast of Africa. However, its close morphological resemblance to *Anditrigonia* Levy, 1967*b*, many species of which have been included (Nakano 1965) in *Megatrigonia*, leaves no doubt as to its ancestry. Although Tashiro (1979) included *Columbitrigonia* and *Megatrigonia conocardiiformis* (Krauss) in the Apiotrigoniinae, their unornamented area and escutcheon suggests better placement in the Megatrigoniinae.

Genus *Megatrigonia* van Hoepen, 1929

Type species. *Megatrigonia obesa* van Hoepen, 1929; by original designation.

Diagnosis

Very large, robust megatrigoniids with nontuberculate flank costae that pinch and swell irregularly without forming discrete nodes. Anterior flank costae strongly oblique, distant.

Megatrigonia conocardiiformis (Krauss, 1843)

Figs 14, 15A–C, 16

Lyriodon conocardiiformis Krauss, 1843: 130.
Lyrodon conocardiiformis Krauss, 1850: 454, pl. 49 (figs 1a–d).
Trigonia conocardiiformis (Krauss) Lycett, 1879: 210, 211, 230. Paulcke, 1903: 309. Kitchin, 1908: 119, pl. 7 (figs 2–4). Lambert, 1944: 392. Stoyanow, 1949: 80. Reyes, 1970: 9.
non *Trigonia* aff. *conocardiiformis* (Krauss) Burckhardt, 1903: 72, pl. 13 (figs 1–2) (= *Anditrigonia eximia* (Philippi)).
non *Trigonia conocardiiformis* Lange (*non* Krauss), 1914: 235, pl. 19 (figs 1a–b) (= *M. staffi* (Lange)).
Trigonia (Megatrigonia) conocardiiformis (Krauss) Rennie, 1936: 332. Leanza, 1941: 232.
Megatrigonia (Megatrigonia) conocardiiformis (Krauss) Cox, 1952: 58. Da Silva, 1966: 68, pl. 4 (fig. 2); Levy, 1967*b*: 136. Nakano, 1965: 17. Cooper, 1979*b*: 58.
Apiotrigonia conocardiiformis (Krauss) Tashiro, 1979: 183.

Fig. 14. *Megatrigonia conocardiiformis* (Krauss), × 1. Left lateral view of the provisional neotype, SAM-PCU1910.

Type

The whereabouts of Krauss' (1843) type material is unknown; it may be necessary to designate a neotype.

Material

A total of 75 specimens were available for study, 70 in the South African Museum, SAM–4642–3, 4644, 4649, 5033–4, 5042, 7107, 7492, 7524, 7494, 7591, 9841–3, 12444–5, D1897, D1898 (11 specimens), D1910 (23 specimens), D1934, D1937, D1939 (3 specimens), D1991, and 12 unnumbered specimens, as well as 5 in the Port Elizabeth Museum, PEM–1464/72, 1463/51 and 3 unnumbered specimens.

Description

Shell very large (maximum length about 165 mm), massive, pyriform, inequilateral, strongly produced posteriorly (H/L = 0,50–0,61). Umbones fairly prominent, rounded, situated about 30 per cent of the shell length from the anterior, with moderately inturned, slightly opisthogyrous beaks. Valves moderately inflated anteriorly (H/W = 0,40–0,57). Anterior margin strongly convex, passing imperceptibly into the broad, gently convex ventral margin; the posterodorsal margin is shallowly concave and the respiratory margin rounded.

The very elongate, lanceolate escutcheon is sunken and smooth. There is a very narrow but rather deep lunule that extends about one-third of the shell height. An escutcheon carina is lacking whereas, beyond about 8 mm from the umbo, the marginal carina passes into a rounded umbonal ridge. The area is narrow, unornamented beyond the nepionic stage, with a prominent longitudinal groove that is closer to the escutcheon than the flank. The nepionic stages show crowded, simple, subconcentric ribs running from the anterior commissure to the marginal carina, where they flex strongly forwards, forming an acute angle with the flank costae, to cross the area obliquely and pass weakly on to the outer part of the escutcheon. Later flank costae are discrepant, with a coarse, robust, distant, strongly oblique anterior set of about 10–13 ribs that pinch and swell irregularly but do not form true nodes. These costae curve strongly upwards posteriorly to become subvertical, whereas anteriorly they may zigzag or break up into pustules; in large specimens they become effaced anteroventrally. Then follow about seven similar ribs that are subvertical and only weakly curved. The posterior set of *c.* 18 costae are narrow, crowded, somewhat undulatory, broader than the interspaces, almost straight, and inclined posteroventrally. Ribbing is effaced posterodorsally, just before reaching the area, to leave a small portion of the flank smooth.

Occurrence

Megatrigonia conocardiiformis (Krauss) is reported from the Upper Tithonian of northern Moçambique, the Upper Valanginian of the Algoa Basin,

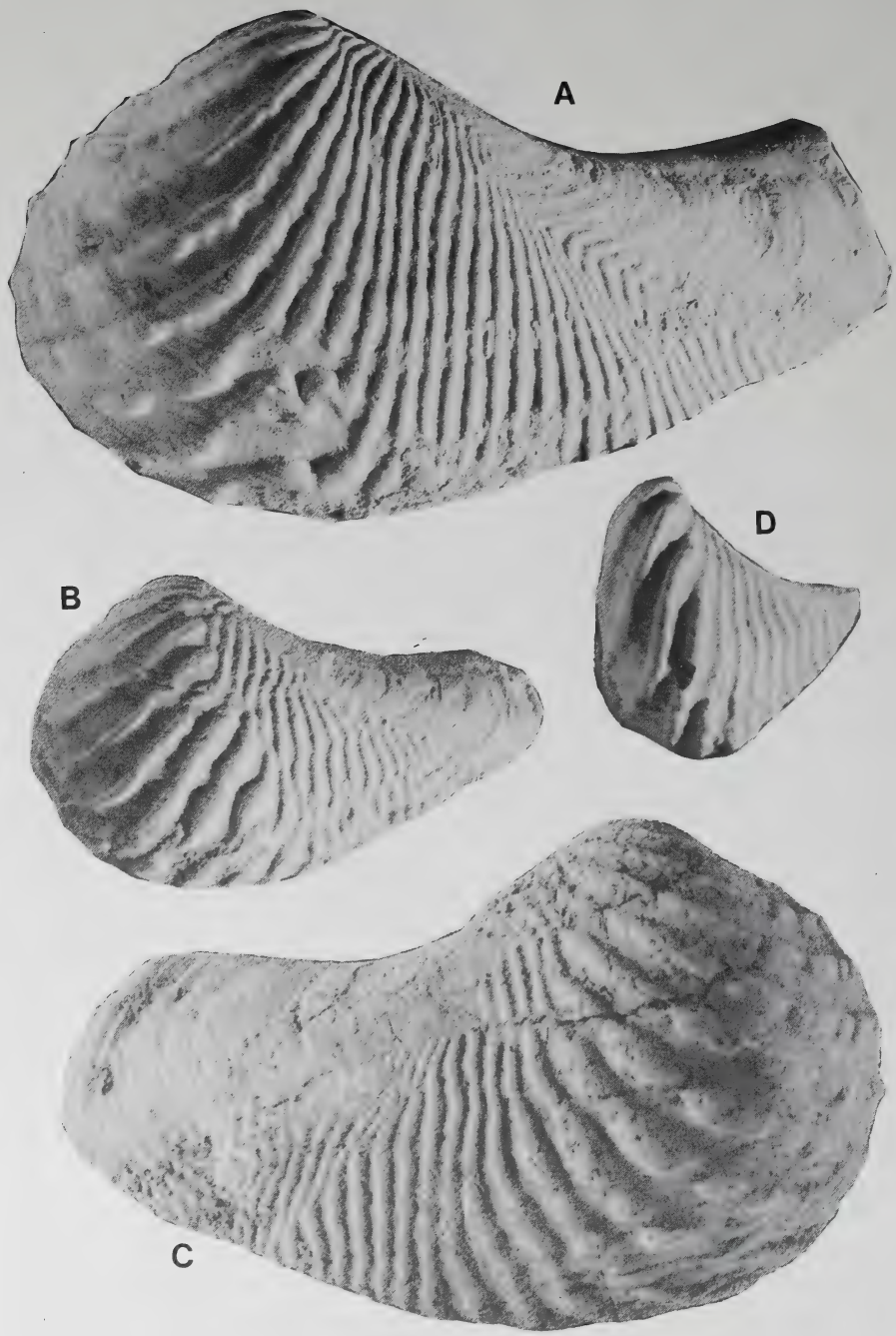

Fig. 15. A–C. *Megatrigonia conocardiiformis* (Krauss). A. Left lateral view of PEM–1463/51, × 1. B. Left lateral view of a specimen in the Port Elizabeth Museum. Note the similarity of this individual to *Pisotrigonia*, the main difference being the more rounded anterior and lack of anterior inflation. C. Right valve of an unnumbered specimen in the Port Elizabeth Museum. D. *Pisotrigonia kraussi* (Kitchin), × 1. Left valve of a juvenile, SAM–PCU7623.

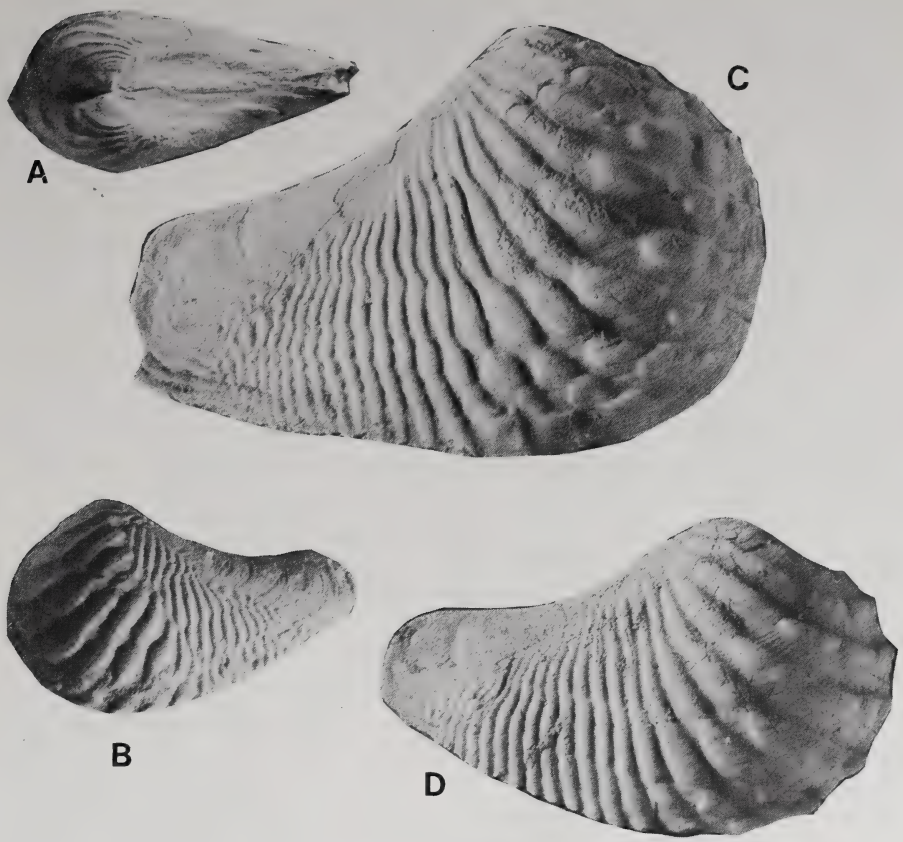

Fig. 16. *Megatrigonia conocardiiformis* (Krauss), × 1. A–B. Dorsal and lateral views of a juvenile, PEM–1464/72. C–D. Right lateral views of two unnumbered topotypes in the Port Elizabeth Museum.

where it is a moderately common element, and from the Robberg Formation, the age of which is under debate but probably late Valanginian.

Subfamily Pterotrigoniinae van Hoepen, 1929

Diagnosis

Small to moderately large megatrigoniids, ovate to club-shaped and posteriorly rostrate; umbones prominent, often with strongly incurved, opisthogyrous beaks; escutcheon sunken, lanceolate, with transverse costellae; escutcheon carina obsolete; marginal carina generally restricted to umbonal region; area crossed by concentric ribs in nepionic stages, later ribbing effaced, oblique, V-shaped or radial; flank costae oblique, prominently tuberculate or finely crenulated, often differentiated into anterior and posterior sets.

Discussion

The earliest representative of the subfamily is *Pisotrigonia* which, at the beginning of the Cretaceous, gave rise to *Pterotrigonia*. The latter, in turn, is believed to have given rise to the Scabrotrigoniini Cooper, 1989, which rose to dominance in the Upper Cretaceous. The Scabrotrigoniini comprise the weakly inflated and lunate pterotrigoniines such as *Ptilotrigonia*, *Scabrotrigonia*, and *Acanthotrigonia*, culminating in *Linotrigonia* in which tuberculation is reduced and the ribs are finely crenulated. *Arabitrigonia* is similar to *Scabrotrigonia* but with a straight dorsal margin, an obliquely truncate respiratory margin, and radial costellae to the nepionic stages of the area. Its relationship to *Scabrotrigonia* is the same as that between *Anditrigonia* and *Paranditrigonia*.

Although there are marked similarities between Apiotrigoniinae and Pterotrigoniinae, including transverse costellae to the area and escutcheon, finely tuberculate costae in some, and an internally crenulated posteroventral margin, the phylogeny depicted by Tashiro (1979) suggests the similarities are the result of convergence.

Genus *Pterotrigonia* van Hoepen, 1929

Type species. *Pterotrigonia cristata* van Hoepen, 1929; by original designation.

Diagnosis

Club-shaped pterotrigoniines, much longer than high, with a concave posterodorsal margin; valves strongly inflated anteriorly, rostrate posteriorly; area smooth in maturity; flank costae conspicuously tuberculate, poorly discriminated into anterior and posterior sets; those to the anterior are curved whereas those to the posterior are straight, inclined, and finely crenulated.

Discussion

The above diagnosis of *Pterotrigonia* is more restricted than that of Cox (1969), since it excludes *Scabrotrigonia*, *Acanthotrigonia*, *Ptilotrigonia* and *Pisotrigonia*, which are regarded as generically distinct. Differences with *Pisotrigonia* are noted below.

Like the genera *Trigonia* and *Myophorella*, there are numerous species of *'Pterotrigonia'* that only vaguely approach the type species and which must, in the future, be assigned, on phyletic grounds, to other taxa. Several representatives in the present fauna fall into this category but, until a more thorough phylogenetic analysis of the genus is attempted, no new names are introduced.

Subgenus *Pterotrigonia* van Hoepen, 1929

Diagnosis

Small to large, generally much longer than high; flank ornament discrepant, with tuberculate anterior set and finely crenulated, straight posterior set.

Pterotrigonia (?Pterotrigonia) knighti (Pringle, 1960)

Figs 17–18

Trigonia knighti Pringle, 1960: 90, pl. 1 (figs 1–3).
Pterotrigonia (Pterotrigonia) knighti (Pringle) Cooper, 1979*b*: 55.

Types

The holotype is in the Port Elizabeth Museum (Figs 17–18). There are two paratypes in the British Museum (Natural History), and a third in the Natal Museum (Pietermaritzburg). The whereabouts of two other specimens referred to by Pringle (1960) is uncertain.

Description

The shell is large (maximum length at least 109 mm), club shaped, as high as long (H/L = 0,99–1,01), massive, strongly inflated anteriorly (W/H = 0,37–0,43) and rostrate posteriorly. The very prominent umbones are subterminal, with strongly inturned, opisthogyrous beaks. The straight, subvertical anterior margin passes evenly into the almost straight ventral margin. The posterodorsal margin is broadly concave and the respiratory margin seems to have been narrowly rounded. The oval, flattened anterior face meets the flanks at prominent anterolateral shoulders.

The escutcheon is very broad, sunken, and extends almost the entire posterodorsal length of the shell. It is ornamented with numerous, finely beaded, transverse costellae that are narrower than the interspaces. The area is narrow, unornamented beyond the nepionic stages and has a persistent longitudinal groove. As in *P. tocaimaana* (Lea), there is a prominent marginal carina that persists to the middle growth stages.

Flank ornament is moderately discrepant. It comprises a flexuous set of about 12, rather coarse, flared anterior costae that curve strongly upwards and extend to the anterior commissure. These ribs are irregularly tuberculate, with 3–4 large tubercles on the anterolateral shoulder. The ten or so costae of the posterior set of ribs are finely crenulated, subparallel, narrower than the interspaces, and meet the posteroventral margin at right angles.

Occurrence

Pterotrigonia (?Pterotrigonia) knighti (Pringle) is known only from the Upper Valanginian of the Algoa Basin, where it is a very rare component of the faunas.

Pterotrigonia rogersi (Kitchin, 1908)

Figs 19–20

Trigonia rogersi Kitchin, 1908: 99, pl. 3 (fig. 3), pl. 4 (fig. 1), pl. 5 (fig. 2).
Pterotrigonia rogersi (Kitchin) Pringle, 1960: 89. Cooper, 1979*b*: 57, fig. 7.
Megatrigonia rogersi (Kitchin) Nakano, 1965: 17.
?Megatrigonia rogersi (Kitchin) Reyes, 1970: 8, pl. 1 (figs 1–2), pl. 3 (fig. 1).

Fig. 17. *Pterotrigonia (?Pterotrigonia) knighti* (Pringle), × 0,71. Lateral and anterior views of the holotype in the Port Elizabeth Museum.

Type

By lectotype designation herein, the original of the specimen figured by Kitchin (1908, pl. 3 (fig. 3), pl. 4 (fig. 1)), SAM–3974 (Fig. 19C).

Material

A total of 108 specimens in the South African Museum, SAM–5088, 12950–53, 12955–58, 12960–62, D1882 (73 specimens) and 22 without number, as well as PEM–1465/61.

Description

Shell moderately large (maximum length 135 mm), strongly inequilateral, moderately inflated anteriorly (W/H = 0,35–0,44), longer than high

Fig. 18. *Pterotrigonia (?Pterotrigonia) knighti* (Pringle), × 1. Dorsal view of the holotype.

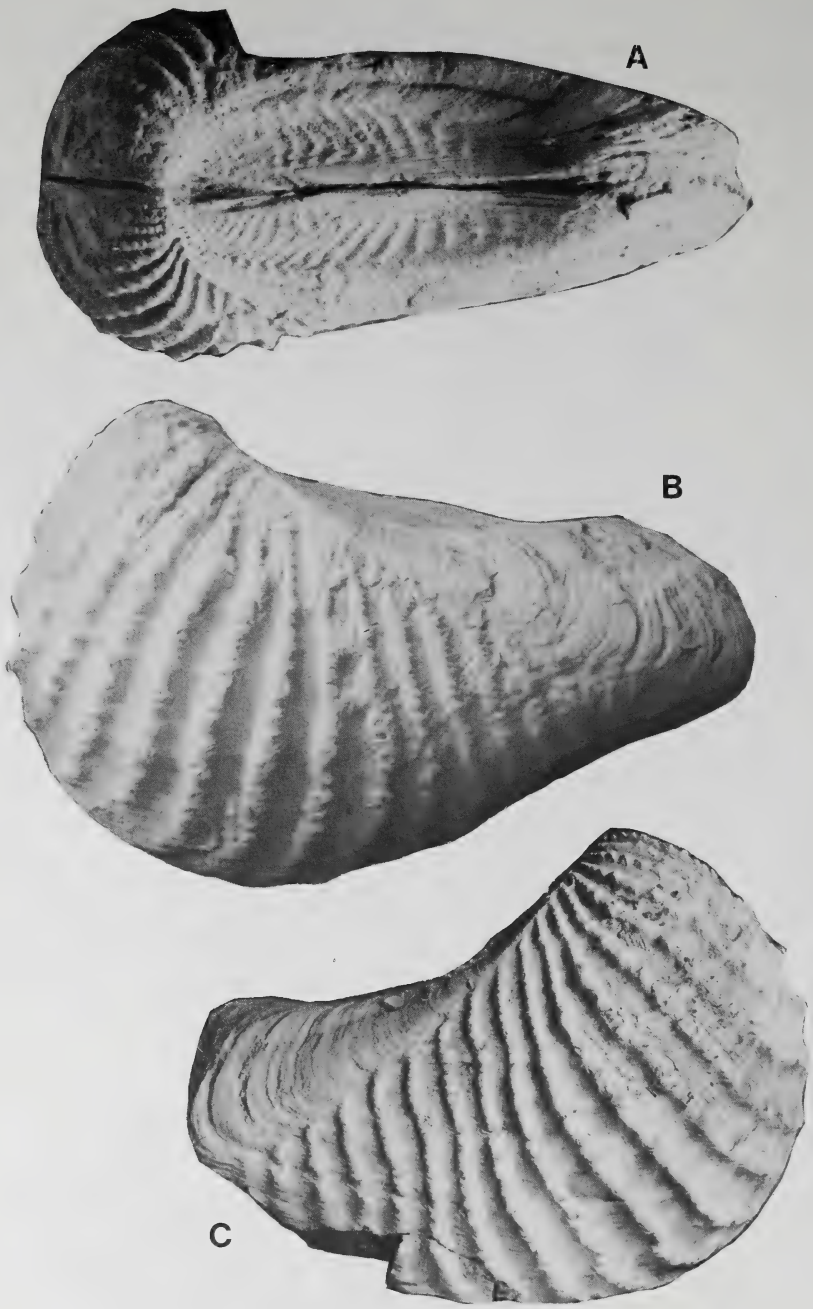

Fig. 19. *Pterotrigonia rogersi* (Kitchin), × 1. A–B. Dorsal and lateral views of PEM–1465/61. C. Lateral view of the lectotype in the South African Museum.

(H/L = 0,63–0,71) and posteriorly produced. Umbones prominent, broad, strongly incurved, situated about one-quarter of the shell length from the anterior, with slightly opisthogyrous beaks. Anterior margin broadly convex, flattish, passing into the very broad, gently convex ventral margin. The posterodorsal margin is shallowly concave, and the respiratory margin subtruncate with a distinct posterior gape.

The ligament pit is about 17 per cent of the shell length. The sunken escutcheon is very broad, conspicuous, lanceolate, with fine, beaded, obliquely transverse costellae that become obsolete before reaching the commissure. In the nepionic stages, the costellae of the escutcheon extend to the median longitudinal groove of the area, giving the inner area a beaded appearance for up to 15 mm from the beak. A beaded marginal carina may extend for the same distance, becoming rounded thereafter. The area is narrow, with a prominent longitudinal groove that persists to maturity and is positioned slightly closer to the escutcheon than the flank. In the nepionic stages it is ornamented by fine, oblique costellae that are more numerous than the flank costae, which they meet at the marginal carina in an anteriorly directed chevron. Beyond 15 mm from the umbo, the area is unornamented.

Fig. 20. *Pterotrigonia rogersi* (Kitchin), × 1. Left valve of a topotype in the South African Museum.

In the nepionic stages the distinctly tuberculate flank costae are subconcentric. Later flank costae are strongly oblique but not sharply discrepant and extend to the anterior commissure. The anterior 12 or so costae are narrower than or as broad as the interspaces, finely but prominently tuberculate, and weakly curved until they reach the anterior face where they curve strongly upwards to meet the anterior commissure almost at right angles. On the posterior half of the flanks the costae are straight, rigid, and inclined slightly to the posterior, with slightly narrower interspaces.

Discussion

The side-by-side occurrence of two species of *Pterotrigonia*, *Pterotrigonia (?Pterotrigonia) knighti* and *P. rogersi* points to an early Neocomian radiation of the Pterotrigoniinae. Although *P. rogersi* does not fall easily into any of the available genera and subgenera, it is referred to *Pterotrigonia* pending further phylogenetic study.

Occurrence

Pterotrigonia rogersi (Kitchin) is a common element in the Upper Valanginian faunas from the Algoa Basin. It may also occur in the Lower Hauterivian of southern Chile.

Genus *Pisotrigonia* van Hoepen, 1929

Type species. *Pisotrigonia salebrosa* van Hoepen, 1929; by original designation.

Diagnosis

Like *Pterotrigonia* but as high as long, often extremely inflated anteriorly and with broadly flattened anterior face. Posterodorsal margin deeply excavate. Umbones very conspicuous, subterminal, with beaks exceptionally incurved, opisthogyrous; escutcheon with transverse costellae, which may be very weak or absent in early representatives; area smooth except in nepionic stages; flank costae markedly discrepant, with generally thick, robust, distant, coarsely tuberculate, anterior costae and narrow, straight, crowded, finely serrated posterior costae. Age: Tithonian–Cenomanian (?Maastrichtian).

Discussion

Although most workers have rejected *Pisotrigonia* as a junior subjective synonym of *Rinetrigonia* (Kobayashi & Nakano 1957; Skwarko 1963; Nakano 1974*b*), the former genus has page priority (Cooper 1988, 1989).

Pisotrigonia ventricosa (Krauss, 1843)

Fig. 21

Lyriodon ventricosa Krauss, 1843: 130.
Lyrodon ventricosus Krauss, 1850: 456, pl. 49 (figs 2c–f only).
Trigonia ventricosa (Krauss) Stoliczka, 1871: 315, pl. 15 (figs 9, 9a). Lycett, 1875: 119, plus text-figure. Müller, 1900: 543, pl. 19 (figs 4–5). Paulcke, 1903: 308. Rogers, 1905: 291, fig. 25,2. Kitchin, 1908: 91, pl. 3 (fig. 1). Woods, 1917: 21. Spath, 1931: 542; 1933: 798. Dietrich, 1938: 97. Stoyanow, 1949: 88. Reyes, 1970: 9.
Rinetrigonia ventricosa (Krauss) van Hoepen, 1929: 22.
Pterotrigonia ventricosa (Krauss) Cox, 1952: 59; 1961: 23. Pringle, 1960: 89.
Pterotrigonia (Rinetrigonia) ventricosa (Krauss) Crickmay, 1932: 461. Kobayashi & Nakano, 1957: 230. Skwarko, 1963: 20; 1966: 99; 1968: 173. Levy, 1967*a*: 102.
non *Trigonia ventricosa* Kitchin (*non* Krauss), 1903: 104, pl. 10 (figs 4–8) (= *P. parva* van Hoepen).
non *Trigonia ventricosa* Etheridge (*non* Krauss), 1907: 76, pl. 1 (figs 7–8) (indeterminate pterotrigoniine).

Type

The whereabouts of Krauss' (1843) type material is unknown; it may be necessary to designate a neotype.

Material

Hundreds of specimens in the South African Museum, many unnumbered or with the Van Hoepen number D1841.

Description

Shell medium sized (maximum length 50 mm), strongly inequilateral, as high as long (H/L = 0,91–1,13), anteriorly extremely inflated (H/W = 0,47–0,54) and rostrate posteriorly. Conjoined valves are wider than long. Umbones very prominent, extremely incurved, with opisthogyrous beaks. Anterior margin weakly curved to almost straight, very high, with broad, flattish anterior face, passing rather sharply into the broad, straight to slightly concave ventral margin. The posterodorsal margin is deeply concave and the narrow respiratory margin rounded.

The escutcheon is broad, deeply sunken, lanceolate, with weak oblique costellae along its outer margin, the inner margin being smooth. In some individuals the escutcheon is entirely ribbed or entirely smooth. Carinae are restricted to the nepionic stage. The area is narrow, bipartite, with oblique costellae in the umbonal region but later smooth.

The flank costae of the nepionic stages are subconcentric, with fine transverse ridges. Later costae are markedly discrepant, divided into a coarse, distant anterior set that curves markedly only on the anterior face to meet the commissure at right angles, and a fine, crowded posterior set. The anterior costae are as wide as or narrower than the interspaces; those closest to the umbo are coarsely tuberculate throughout. Posteriorly, however, the coarse rounded tuberculation is increasingly restricted to the ventral part of the costa, leaving the dorsal extension as a thin, wavy, vertical, finely crenulated costella. It is with final loss of coarse tuberculation that the change to the posterior set occurs in which the wavy, crowded, subvertical costellae are finely crenulated throughout. There are about 10–12 costae in the anterior set and 8–12 in the posterior set.

Discussion

Kitchin (1903: 104, pl. 10 (fig. 4)) identified material from the Tithonian of Cutch with *T. ventricosa* (Krauss). Van Hoepen (1929: 38), however, considered the anterior ribs of the Cutch species to be too coarse, with larger and more prominent nodes, and the posterior ribs too uneven for assignment to *T. ventricosa*. Consequently, he renamed the Cutch species *Pisotrigonia parva* (Fig. 22). Although Rennie (1936) was highly critical of Van Hoepen's (1929) taxonomy, the writer has—through the courtesy of Drs N. J. Morris and R. J. Cleevely, studied topotype material of *P. parva* van Hoepen and concurs that it is a distinctive Tithonian species. Also closely allied is *Pisotrigonia tuberculifera*

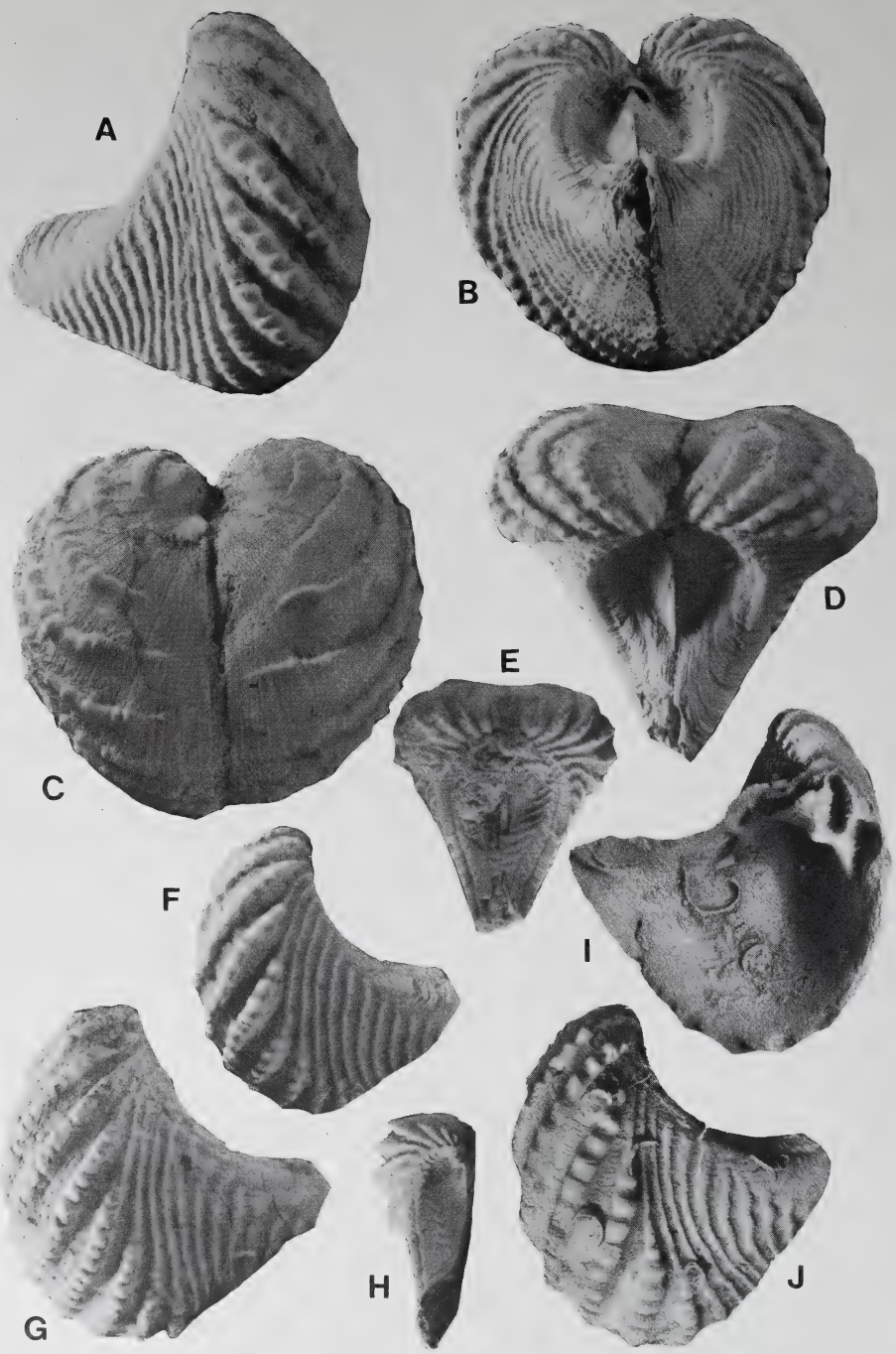

Fig. 21. *Pisotrigonia ventricosa* (Krauss), × 1. A–D. Lateral, posterior, anterior and dorsal views of the provisional neotype. E–F. Dorsal and lateral views of a topotype. G–H. Lateral and dorsal views of a topotype. I–J. Internal and external views of a left valve. All the specimens are in the South African Museum.

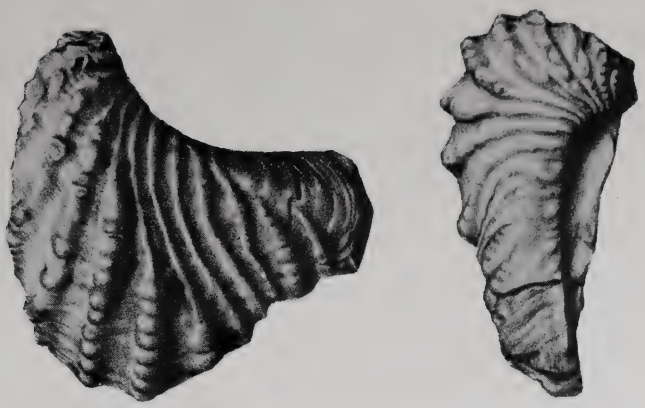

Fig. 22. *Pisotrigonia parva* van Hoepen, × 1. The holotype (after Kitchin 1903).

(Stoliczka) (1871: 315, pl. 15 (figs 10–12)), which was said to differ '. . . by being of a more regularly rounded triangular shape, less attenuated and produced posteriorly, and possessing a narrower and not so deeply excavated area' (Stoliczka 1871: 315).

Occurrence

Pisotrigonia ventricosa (Krauss) abounds in the Upper Valanginian of south-east Africa. It questionably also occurs in the Tithonian of India (Cutch) and East Africa (Tanzania).

Pisotrigonia kraussi (Kitchin, 1908)

Figs 15D, 23

Lyrodon ventricosus Krauss, 1850, pl. 2 (fig. 2a–b only).
Trigonia kraussi Kitchin, 1908: 95, pl. 3 (fig. 2).
Rinetrigonia kraussi (Kitchin) van Hoepen, 1929: 22.
Pterotrigonia (Rinetrigonia) kraussi (Kitchin) Kobayashi & Nakano, 1957: 230, fig. 1. Skwarko, 1968: 174.

Type

The holotype is, by monotypy, the original of the specimen figured by Kitchin (1908, pl. 3 (fig. 2)) (Fig. 23), in the South African Museum.

Material

In addition to the holotype (SAM–3999), there are three other specimens in the South African Museum, SAM–D1942 and D1883 (2 specimens).

Description

Shell large (maximum length about 90 mm), higher than long (H/L = 0,82), strongly inequilateral, extremely inflated anteriorly (H/W = 0,54) and rostrate

posteriorly. Umbones very prominent, massive, subterminal, with extremely incurved, opisthogyrous beaks. The anterior margin is very high, weakly convex, and with a very broad, flattened anterior face. It passes rather abruptly into the straight to shallowly concave ventral margin. The posterodorsal margin is markedly concave and the respiratory margin presumably narrowly rounded. The anterolateral shoulders protrude significantly beyond the anterior commissure.

The escutcheon is relatively broad and deeply excavate, without oblique costellae. The marginal carina is restricted to the nepionic stages, quickly becoming rounded and indistinct. The area is very narrow, with a prominent longitudinal groove, and lacks ornament for much of its growth.

On the nepionic stages the flank costae are subconcentric. Later they become strongly oblique and markedly discrepant. The eight ribs of the anterior series are very robust, exaggerated, narrower than the interspaces, almost straight, but curving upwards on the anterior face. They are generally coarsely tuberculate but on SAM–D1942 the anterior costae seem to be nontuberculate. These anterior ribs approach the anterior commissure obliquely but pinch out before reaching it; the anteroventral ribs are the first to reach the commissure, which they contact at right angles. The finely crenulated, crowded costellae of the posterior series are initially subvertical, but become increasingly inclined to the posterior, and are about as narrow as the interspaces.

Fig. 23. *Pisotrigonia kraussi* (Kitchin), × 1. Lateral and anterior views of the holotype in the South African Museum.

Occurrence

Pisotrigonia kraussi (Kitchin) is a very rare component in the Upper Valanginian faunas of south-east Africa.

Family **Iotrigoniidae** Saveliev, 1958

(*nom. transl.* herein *ex* subfamily Iotrigoniinae Saveliev, 1958).

Diagnosis

Medium to large megatrigoniaceans; pyriform to subovate; posteriorly strongly produced, inequilateral; respiratory margin narrowly rounded to obliquely truncate; escutcheon crossed by weak transverse costellae in nepionic stage, later smooth; carinae generally restricted to nepionic stage; area narrow, bipartite, smooth except in earliest growth stages; flanks with generally fine subconcentric costae anteriorly meeting fewer, broader, subvertical posterior costae in a chevron; ornament may be replaced by concentric growth rugae in maturity.

Discussion

Although this taxon is included by many within the synonymy of the Megatrigoniinae, the subfamily is present already in the Upper Bajocian of Argentina, contemporaneous with the most primitive megatrigoniines, i.e. *Anditrigonia kiedeli* (Weaver) (Leanza & Garate 1987). Since *Iotrigonia* persists into the Maastrichtian of New Zealand (Fleming 1964, 1987) it is an important phyletic line that merits recognition. Its origins are cryptic. Saveliev (1958) suggested derivation from Vaugoniidae of the Myophorellacea, but the writer follows Kitchin (1903) in regarding the similarities as due to convergence. The importance of V-shaped flank costae to primitive Megatrigoniinae, together with a smooth escutcheon and impersistent carinae, suggests a common ancestry for the Iotrigoniinae and Megatrigoniinae.

Genus *Iotrigonia* van Hoepen, 1929

Type species. *Iotrigonia crassitesta* van Hoepen, 1929; by original designation.

Diagnosis

Area unornamented beyond the nepionic stages and with a rounded respiratory margin. Anterior flank costae often irregular, zigzagging, pinching and swelling, and forming prominent tubercles at the anterolateral shoulder in some; anterior face smooth; chevrons persist to large size but may become effaced in maturity when they are replaced by concentric growth rugae.

Discussion

The earliest species to be assigned to *Iotrigonia* is *I. radixscripta* (Lambert) (1944: 369, pl. 1 (figs 7–8), pl. 6 (fig. 1); Leanza & Garate 1987: 225, pl. 2

(fig. 7)) from the mid-Bajocian to early Callovian of Argentina. This species differs in several noteworthy aspects from typical *Iotrigonia*, notably in its straight posterodorsal margin, obliquely truncate respiratory margin, relatively prominent marginal carina, and the presence of a carina marking the longitudinal furrow to the area, as well as conspicuous growth rugae to the adult area. These differences are here considered to warrant generic separation and the name *Lambertiella* is proposed, with *Trigonia radixscripta* Lambert as type species. *Iotrigonia* attained a near-cosmopolitan distribution in the Tithonian–Neocomian. In the Australasian province it gave rise to *Zaletrigonia* Skwarko, 1963, which is distinguished by the rapid replacement of chevrons by two sets of oblique ribs that converge ventrally but do not meet.

Iotrigonia vau (Sharpe, 1856)

Fig. 24

Trigonia vau Sharpe, 1856: 194, pl. 22 (fig. 5). Tate, 1867, pl. 7 (fig. 8). Paulcke, 1903: 309. Kitchin, 1903: 67; 1908: 110, pl. 6 (figs 1–3). Stoyanow, 1949: 79. Skwarko, 1963: 17. Reyes, 1970: 12.
Iotrigonia vau (Sharpe) van Hoepen, 1929: 9. Nakano, 1965: 19.
Trigonia (Iotrigonia) vau Sharpe. Rennie, 1936: 343.
Megatrigonia (Iotrigonia) vau (Sharpe) Cox, 1952: 58. Pringle, 1960: 89.
Iotrigonia cf. *vau* (Sharpe) Cooper, 1979*b*: 52, fig. 2.

Type

By lectotype designation herein, the original of the specimen figured by Sharpe (1856, pl. 22 (fig. 5)).

Material

In addition to 25 specimens available for study in the South African Museum, SAM–653, 4645, 4650–2, 4655, 5039–40, 5089, 7454, 7567, 7569, 7571, 7572 (2 specimens), 7573–74, 7575 (2 specimens), 7595, 12776, D574, D1944 and two unnumbered specimens, there are also several unnumbered specimens in the Port Elizabeth Museum.

Description

Shell medium sized (maximum length about 65 mm), trigonally ovate, elongate (H/L = 0,52–0,61), with the moderately elevated umbones situated about one-third of the shell length from the anterior. The posterodorsal margin is shallowly concave, the anterior margin strongly convex passing imperceptibly into the broadly convex ventral margin, and the respiratory margin narrowly rounded. The valves are moderately inflated anteriorly (H/W = 0,33–0,36).

The sunken escutcheon is narrow, lanceolate, smooth, and extends about 50 per cent of the posterodorsal shell length. It rises slightly at the commissure. The area is narrow, smooth beyond the nepionic stages, and with a longitudinal groove that weakens and may become obsolete posteriorly. Inner and marginal

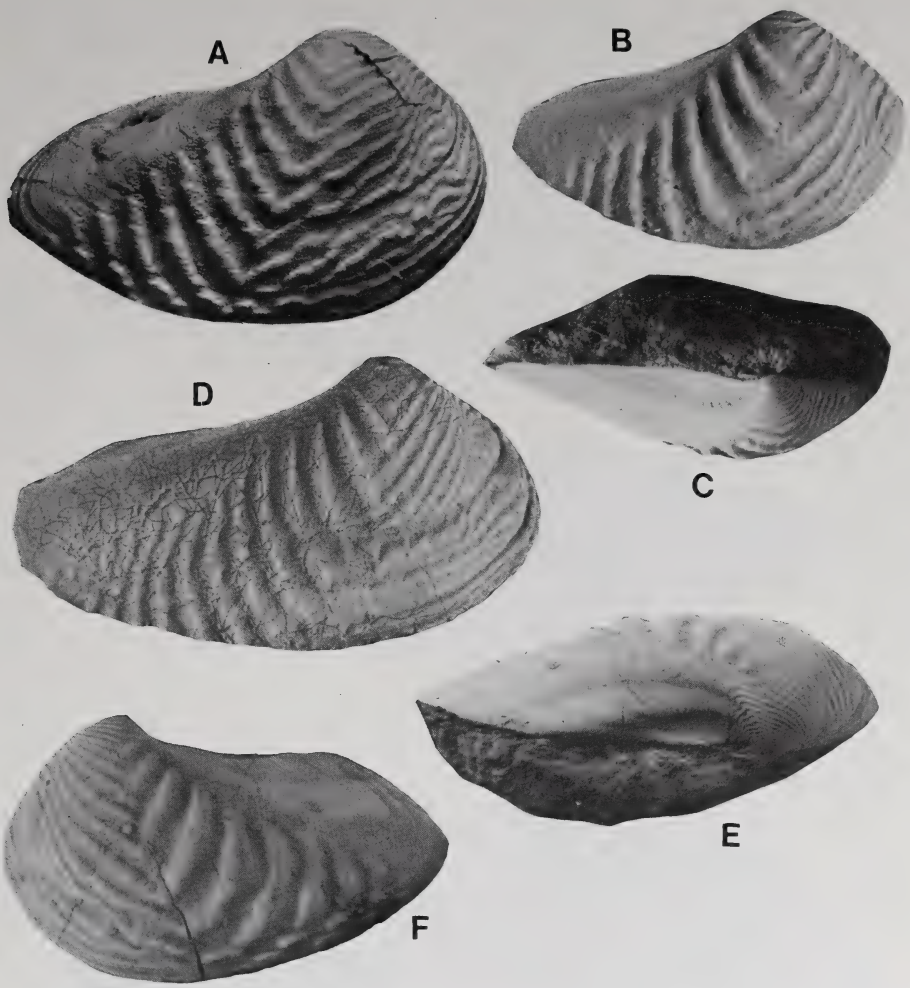

Fig. 24. *Iotrigonia vau* (Sharpe), × 1. A. Lateral view of the specimen in the South African Museum figured by Kitchin (1908). B–C. Lateral and dorsal views of a right valve in the Port Elizabeth Museum. D. Right valve of a posteriorly elongate individual in the Port Elizabeth Museum. E–F. Lateral and dorsal views of a left valve in which the posterior branches of the flank costae are unusually swollen.

carinae are lacking. The area is ornamented by transverse costellae for about 7 mm from the beak, after which the ribs are restricted to the angulation separating the area and escutcheon.

The flank ornament of the nepionic stages, up to a distance of 10 mm from the umbones, comprises fine concentric ribs, about as wide as the interspaces. These pass obliquely across the area with a slight inflexion at the position of the marginal carina, and continue weakly on to the outer edge of the escutcheon.

Beyond this stage the adult ornament is developed abruptly, with the flank costae forming deep chevrons whose axial trace is inclined to the posterior. The broad, low, ribs of the posterior branches are much wider than the interspaces and, except perhaps at the extreme posterior, are directed anteroventrally. The much finer oblique ribs of the anterior branches meet the posterior ribs almost at right angles in a ratio of 3 : 2 in the later growth stages. Anteriorly the ribs bend sharply upwards and become sinuous, with irregular zigzags, but become obsolete on the anterolateral shoulder, leaving the anterior face impressed only by growth striae. The flank chevrons become obsolete at the largest growth stages, when the anterior branches form coarse concentric growth rugae that interfere with and crenulate the posterior ribs, giving them a nodate appearance. Anteroventrally the ribs become irregular, zigzagging and pinching and swelling.

Occurrence

Iotrigonia vau (Sharpe) is a common element in the late Valanginian faunas of south-east Africa. It is probably also present in the Robberg Formation, and has been reported from the Tithonian of East Africa.

Iotrigonia stowi (Kitchin, 1908)

Fig. 25

Trigonia sp. Kitchin, 1903: 74.
Trigonia stowi Kitchin, 1908: 115, pl. 6 (figs 4–5), pl. 7 (fig. 1).
Iotrigonia stowi (Kitchin) van Hoepen, 1929: 8. Nakano, 1965: 19. Cooper, 1979*b*: 52, fig. 4.
Trigonia (Iotrigonia) stowi (Kitchin) Rennie, 1936: 343.
Megatrigonia (Iotrigonia) stowi (Kitchin) Cox, 1952: 58. Pringle, 1960: 89.
?Iotrigonia stowi (Kitchin) Reyes, 1970: 11, pl. 2 (fig. 3).
?Iotrigonia stowi var. *aisenensis* Reyes, 1970: 13, pl. 2 (figs 1–2).

Type

By lectotype designation herein, the original of the specimen figured by Kitchin (1908, pl. 6 (fig. 5)), SAM–PCU3979 (Fig. 25A).

Material

Two unnumbered specimens in the South African Museum, as well as PEM–1465/62 and AM–721.

Description

Shell moderately large (maximum length about 110 mm), very elongate (H/L = 0,52), variable in outline, but typically subtrapezoidal, with weakly inflated valves (H/W = 0,16). The fairly prominent umbones are situated between one-quarter and one-third of the shell length from the anterior, and the beaks are weakly incurved and slightly opisthogyrous. The posterodorsal margin is shallowly concave, almost straight and forms an obtuse angle with the straight, strongly produced anterior border. The long ventral margin is gently convex and the siphonal margin narrowly rounded.

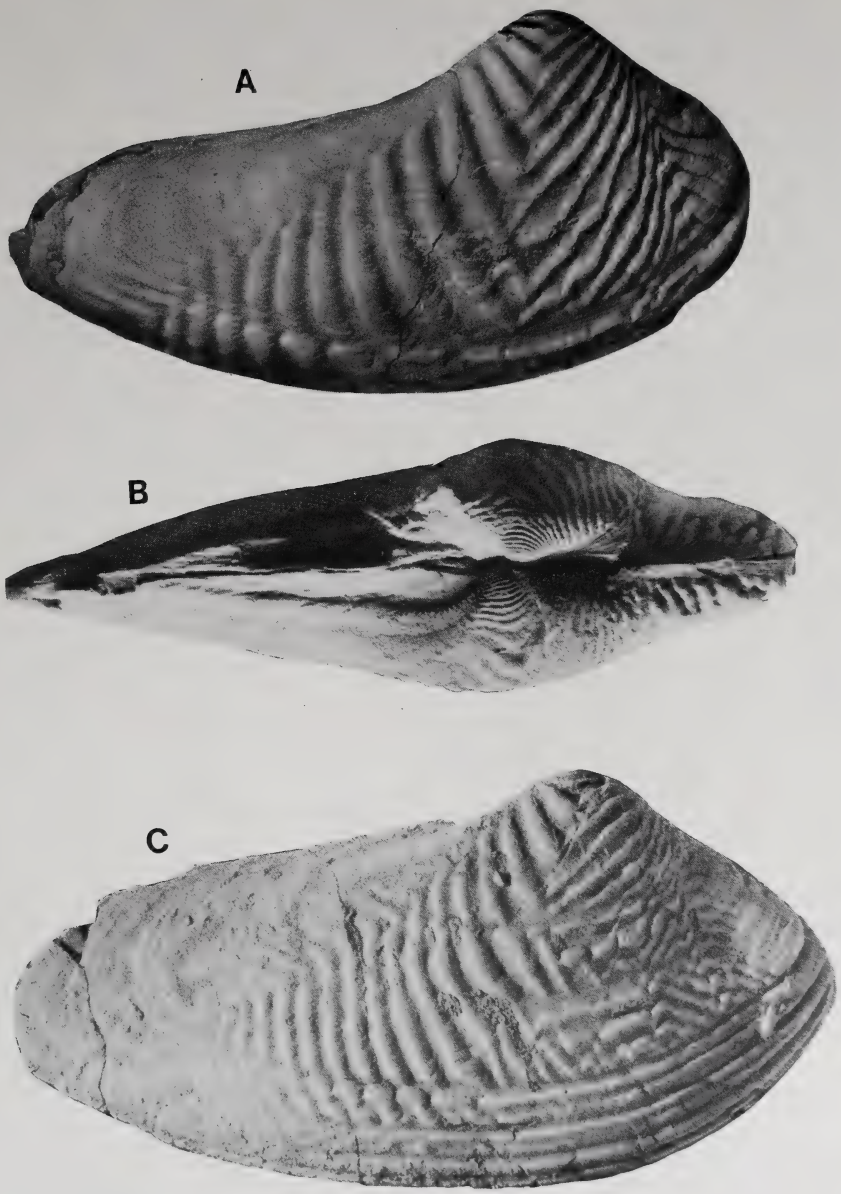

Fig. 25. *Iotrigonia stowi* (Kitchin), × 1. A. Lateral view of right valve figured by Kitchin (1908). B–C. Dorsal and lateral views of a specimen in the Port Elizabeth Museum. Note the swollen tubercles near the anteroventral margin.

The escutcheon is relatively long, lanceolate, shallowly concave, and smooth. The ligament pit is relatively short and broad. The area is narrow, convex, and with a pronounced longitudinal furrow that persists to maturity. Marginal and inner carinae are lacking at all observable growth stages.

The flank ornament of the nepionic stages comprises fine concentric ribs that cross the line of the marginal carina with an inflexion and continue across the area and escutcheon. The adult flank costae form deep acute chevrons whose axial trace curves posteriorly, the anterior branches being fine and oblique whereas the posterior branches are broad, low, and directed anteroventrally. The number of ribs in the two branches are approximately equal, although an occasional rib may be intercalated anteriorly. In maturity the anterior costae become relatively broad, swollen, and irregular, zigzagging and forming upwardly directed chevrons, or breaking into weak nodes. In some individuals ribbing becomes obsolete anteroventrally. Close to the ventral border the posterior ribs are intersected by deep, irregularly developed growth striae causing them to break up into weak nodes. Large specimens show exaggerated swollen tubercles anteroventrally that replace the zigzagging costae.

Occurrence

Iotrigonia stowi (Kitchin) is a rare element in the Upper Valanginian faunas of south-east Africa. It may also occur in the Lower Hauterivian of southern Chile.

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I thank Drs M. A. Cluver and H. C. Klinger for access to the collections of the South African Museum, Mr W. Holleman for allowing me to study the collections of the Albany Museum, Grahamstown, and Mr Barney Newman for assistance with the collections of the Port Elizabeth Museum. Drs E. Pérez d'Angelo (Santiago) and M. Tashiro (Kochi) critically reviewed the manuscript, for which I am grateful, and Betsie Greyling provided general assistance.

REFERENCES

Burckhardt, C. 1903. Beiträge zur Kenntniss der Jura- und Kreideformation der Cordillere. *Palaeontographica* (B) **50**: 1–145.

Cooper, M. R. 1979*a*. A new species of *Myophorella* (Bivalvia, Trigoniidae) from the Sunday's River Formation, South Africa. *Annals of the South African Museum* **78** (3): 21–27.

Cooper, M. R. 1979*b*. Cretaceous Trigoniidae (Mollusca, Bivalvia) from the Brenton Formation, Knysna. *Annals of the South African Museum* **78** (6): 49–67.

Cooper, M. R. 1981. Revision of the late Valanginian Cephalopoda from the Sundays River Formation of South Africa, with special reference to the genus *Olcostephanus*. *Annals of the South African Museum* **83** (7): 147–366.

Cooper, M. R. 1983. The ammonite genus *Umgazaniceras* in the Sundays River Formation. *Transactions of the Geological Society of South Africa* **86** (1): 63–64.

Cooper, M. R. 1988. A new species of trigoniid bivalve from the Lower Cretaceous (Albian) of Zululand. *South African Journal of Geology* **91** (3): 326–328.

COOPER, M. R. 1989. The Gondwanic bivalve *Pisotrigonia* (family Trigoniidae), with a description of a new species. *Paläontologische Zeitschrift* **63** (3/4): 241–250.

COX, L. R. 1952. Notes on the Trigoniidae with outlines of a classification of the family. *Proceedings of the Malacological Society of London* **29** (2–3): 45–70.

COX, L. R. 1961. The molluscan fauna and probable Lower Cretaceous age of the Nanutarra Formation of Western Australia. *Bulletin. Bureau of Mineral Resources, Geology and Geophysics, Australia* **61**: 1–39.

COX, L. R. 1969. Trigoniacea Lamarck, 1859. *In:* MOORE, R. C. *ed. Treatise on invertebrate paleontology. Part N, Mollusca* **6** (1): N471–N489. Boulder: Geological Society of America; Lawrence: University of Kansas.

CRICKMAY, C. H. 1930. The Jurassic rocks of Ashcroft, British Columbia. *University of California Publications in Geological Sciences* **19** (2): 23–74.

CRICKMAY, C. H. 1932. Contributions toward a monograph of the Trigoniidae. *American Journal of Science* **24** (5): 443–464.

DARRAGH, T. A. 1986. The Cainozoic Trigoniidae of Australia. *Alcheringa* **10** (1): 1–34.

DIETRICH, W. O. 1933. Das Muster der Gattung *Trigonia* (Moll. Lam.). *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* **1933** (2): 326–332.

DIETRICH, W. O. 1938. Lamelibranquios cretacicos de la Cordillera Oriental. *Estudios geológicos y paleontológicos sobre la Cordillera oriental de Colombia* **1934** (3): 81–108.

ETHERIDGE, R. 1907. Cretaceous fossils of Natal. Part II. The Umsinene River deposits, Zululand. *Report of the Geological Survey of Natal and Zululand* **3**: 67–90.

FLEMING, C. A. 1964. History of the bivalve family Trigoniidae in the south-west Pacific. *Australian Journal of Science* **26** (7): 196–204.

FLEMING, C. A. 1987. New Zealand Mesozoic bivalves of the superfamily Trigoniacea. *Palaeontological Bulletin. Geological Survey* **53**: 1–104.

FRENEIX, S. 1958. Contribution á l'étude des lamellibranches du Crétacé de Nouvelle-Calédonie. *Sciences de la terre* **4** (3/4): 153–207.

GOLDFUSS, A. 1826–44. *Petrefacta Germaniae tam ea, quae in museo universitatis regiae Borussicae Friedericiae Wilhelminae Rhenanae servantur quam alia quaecunque in museis Hoeninghusiano Muensteriano aliisque extant, iconibus et descriptionibus illustrata. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzenden Länder unter Mitwirkung des Herrn Grafen Georg zu Münster.* Part 2: 1–312. Düsseldorf: Arnz & Co.

HATCH, F. H. & CORSTORPHINE, G. S. 1905. *The geology of South Africa.* Edinburgh: Oliver and Boyd.

HENNIG, W. 1966. *Phylogenetic systematics.* Urbana: University of Illinois Press.

HIRSCH, F. 1980. Jurassic bivalves and gastropods from northern Sinai and southern Israel. *Israel Journal of Earth Sciences* **28** (4): 128–163.

HOLUB, E. & NEUMAYR, M. 1881. Über einige fossilien aus der Uitenhage-Formation in Südafrika. *Denkschriften der Akademie der Wissenschaften* (Math.-nat. Klasse) **44**: 267.

KITCHIN, F. L. 1903. The Jurassic fauna of Cutch. The Lamellibranchiata. Genus Trigonia. *Memoirs of the Geological Survey of India. Palaeontologica indica* (9) **3** (2): 1–122.

KITCHIN, F. L. 1908. The invertebrate fauna and palaeontological relations of the Uitenhage Series. *Annals of the South African Museum* **7** (2): 21–250.

KOBAYASHI, T. 1954. Studies on the Jurassic trigonians in Japan. Part I. Preliminary notes. *Japanese Journal of Geology and Geography* **15** (1/2): 61–80.

KOBAYASHI, T. & AMANO, M. 1955. On the Pseudoquadratae Trigonians, *Steinmannella*, in the Indo-Pacific Province. *Japanese Journal of Geology and Geography* **26** (3/4): 193–208.

KOBAYASHI, T. & NAKANO, M. 1957. On the Pterotrigoniinae. *Japanese Journal of Geology and Geography* **28** (4): 219–238.

KOBAYASHI, T. & TAMURA, M. 1957. Additional new genera and species of trigonians from the Jurassic of Soma, North Japan. *Japanese Journal of Geology and Geography* **28** (1): 35–42.

KRAUSS, F. 1843. Über die geologischen Verhältnisse der östlichen Küste des Kaplandes. *Amtlicher Berichte der Gesellschaft fur Deutsch-Naturforschungs der Aertze* **1843**: 126.

KRAUSS, F. 1850. Über einige petrefacten aus der untern Kreide des Kaplandes. *Nova Acta Acadamiae Caesareae Leopoldino Carolinae germanicae naturae curiosorum* **22** (2): 439–464.

LAMBERT, L. R. 1944. Algunas Trigonias del Neuquén. *Revista del Museo de La Plata* (Paleontologia) (n.s.) **2** (14): 357–397.

LANGE, E. 1914. Die Brachiopoden, Lamellibranchiaten und Anneliden der *Trigonia schwarzi*-Schicht, nebst verleichender Übersucht der Trigonien der gesamten Tendaguru-schichten. *Archiv für Biontologie* **3** (4): 193–289.

LEANZA, A. F. 1941. Dos neuvas Trigonias en el Titonense de Carrín-curá, en el territorio del Neuquen. *Notas del Museo de La Plata* (Paleontologia) **3** (31): 225–233.

LEANZA, A. F. 1942. Los Pelecípodos del Lias de Piedra Pintada en el Neuquén Instituto del Museo de la Universidad Nacional de la Plata. *Revista del Museo de la Plata* (Palaeontologia) (n.s.) **2** (10): 145–206.

LEANZA, H. A. 1981. Una nueva especie de *Myophorella* (Trigoniidae–Bivalvia) del Cretácico Inferior de Neuquén, Argentina. *Ameghiniana* **18** (1/2): 1–9.

LEANZA, H. A. & GARATE, J. I. 1987. Faunas de Trigonias (Bivalvia) del Jurásico y Cretácico Inferior de la Provincia del Nequén, Argentina, conservadas en el Museo Juan Olsacher de Zapala. *In:* VOLKHEIMER, W. *ed. Bioestratigrafia de los Sistemas Regionales del Jurásico y Cretácico de América del Sur* **1**: 201–255. Mendoza.

LEVY, R. 1967*a*. Revision de las Trigonias de Argentina. Parte III. Los Pterotrigoniinae de Argentina. *Ameghiniana* **5** (4): 101–107.

LEVY, R. 1967*b*. Revision de las Trigonias de Argentina. Parte IV. Los Megatrigoniinae de Argentina y su relacion con *Anditrigonia* gen. nov. *Ameghiniana* **5** (4): 135–144.

LEVY, R. 1969. Revision de las Trigonias de la Argentina. Part V: El grupo de las pseudoquadratae. *Ameghiniana* **6** (1): 65–68.

LYCETT, J. 1872–79. A monograph of the British fossil trigoniae. *Monograph of the Palaeontological Society*: 1–52 (1872); 53–92 (1874); 93–148 (1875); 149–204 (1877); 205–245 (1879).

MCLACHLAN, I. & MCMILLAN, I. 1979. Microfaunal biostratigraphy, chronostratigraphy and history of Mesozoic and Cenozoic deposits on the coastal margin of South Africa. *Special Publications. Geological Society of South Africa* **6**: 161–181.

MÜLLER, G. 1900. Versteinerungen des Jura und der Kreide. *In:* BORNHARDT, W. *ed. Zur Oberflächengestaltung und Geologie Deutsch-Ostafrikas. Deutsch-Ost-Afrika* **7**: 514.

NAKANO, M. 1961. On the Trigoniinae. *Journal of Science of the Hiroshima University* (C, Geology and Mineralogy) **4** (1): 71–94.

NAKANO, M. 1965. On the Megatrigoniinae. *Journal of Science of the Hiroshima University* (C, Geology and Mineralogy) **5** (1): 13–20.

NAKANO, M. 1968. On the Quadratotrigoniinae. *Journal of Science of the Hiroshima University* (C, Geology and Mineralogy) **39** (1): 27–41.

NAKANO, M. 1970. Notes on the Trigoniinae and the Nototrigoniinae. *Research Bulletin. Hiroshima Institute of Technology* **4** (1): 91–108.

NAKANO, M. 1971. A note on *Trigonia calderoni* Castillo & Aguilerae. *Research Bulletin. Hiroshima Institute of Technology* **6** (1): 11–13.

NAKANO, M. 1974*a*. A new genus *Mediterraneotrigonia* nov. *Research Bulletin. Hiroshima Institute of Technology* **9**: 77–80.

NAKANO, M. 1974*b*. *Rinetrigonia* and its allies. *Journal of Science of the Hiroshima University* (C, Geology and Mineralogy) **7** (2): 101–111.

NAKANO, M. & NUMANO, K. 1961. On some Gyliakian Pterotrigoniae from Kyushu and Hokkaido, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* (n.s.) **43**: 89–98.

NEWELL, N. D. & BOYD, D. W. 1975. Parallel evolution in early trigoniacean bivalves. *Bulletin of the American Museum of Natural History* **154** (2): 53–162.

PAULCKE, W. 1903. Ueber die Kreideformation in Südamerika und ihre Beziehungen zu anderen Gebieten. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. Beilagebände* **17**: 252–312.

PÉREZ D'A., E. & REYES, B. R. 1983. *Paranditrigonia*, subgénero nuevo de *Anditrigonia* Levy (Mollusca; Bivalvia). *Revista Geológica de Chile* **19–20**: 57–79.

POULTON, T. P. 1977. Early Cretaceous trigoniid bivalves of Manning Provincial Park, southwestern British Columbia. *Geological Survey Paper. Mines and Geology Branch, Canada* **76–9**: 1–25.

POULTON, T. P. 1979. Jurassic trigoniid bivalves from Canada and the western United States of America. *Bulletin. Geological Survey of Canada* **282**: 1–82.

PRINGLE, J. A. 1960. A new species of *Trigonia* from the Sundays River Beds of the Uitenhage Series, Cape Province. *Annals of the Natal Museum* **15** (8): 89–92.

RENNIE, J. V. L. 1936. Lower Cretaceous Lamellibranchia from northern Zululand. *Annals of the South African Museum* **31** (3): 277–391.

RENNIE, J. V. L. 1947. Aptian fossils from Chalala near Lourenço Marques. *Boletim. Serviços de (Indústria), Minas e Geologia. Colónia de Moçambique. Lourenço Marques* **9**: 1–81.

REYES, B. R. 1970. La fauna de Trigonias de Aisen. *Boletin. Instituto de Investigaciones Geológicas, Chile* **26**: 5–40.

REYES, B., R. & PÉREZ D'A., E. 1982. El género *Anditrigonia* Levy, 1967 (Mollusca; Bivalvia) en Chile. *III Congreso Geológico Chileno, 1982*, Concepcion: A289–A301.

REYES, B. R., SEREY, E. T. & PÉREZ D'A., E. 1981. Estudio sistemático y filogenético de las especies sudamericanas del género *Steinmannella* (Trigoniidae; Bivalvia). *Revista Geológica de Chile* **12**: 25–47.

ROGERS, A. W. 1905. *An introduction to the geology of the Cape Colony*. With a chapter on the fossil reptiles of the Karroo Formation by R. Broom. London: Longmans, Green & Co.

SAUL, L. R. 1979. The North Pacific Cretaceous trigoniid genus *Yaadia*. *University of California Publications in Geological Sciences* **119**: 1–65.

SAVELIEV, A. A. 1958. The Lower Cretaceous trigoniids of Mangyschlak and western Turkmenia. *Trudy Vsesoyuznogo Neftyanogo-Issledovatel'skogo Geologicheskikh Instituta (VNIGRI)* **125**: 1–516. (In Russian.)

SHARPE, D. 1856. Description of fossils from the secondary rocks of Sundays River and Zwartkops River, South Africa. *Transactions of the Geological Society. London* (2) **7**: 193–215.

SHONE, R. W. 1976. The sedimentology of the Mesozoic Algoa Basin. Unpublished M. Sc. thesis, University of Port Elizabeth, South Africa.

SILVA, G. H. DA. 1966. Sobre a ocorrência do Jurássico marinho no norte de Moçambique. *Revista dos Estudios Gerais Universitários de Moçambique*(6) **3**: 61–68.

SKWARKO, S. K. 1963. Australian Mesozoic trigoniids. *Bulletin. Bureau of Mineral Resources, Geology and Geophysics, Australia* **67**: 1–55.

SKWARKO, S. K. 1966. Cretaceous stratigraphy and palaeontology of the Northern Territory. *Bulletin. Bureau of Mineral Resources, Geology and Geophysics, Australia* **73**: 96–104.

SKWARKO, S. K. 1967. Mesozoic Mollusca from Australia and New Guinea. 2A. First report of Upper Triassic and ?Lower Jurassic marine molluscs from New Guinea. *Bulletin. Bureau of Mineral Resources, Geology and Geophysics, Australia* **75**: 39–82.

SKWARKO, S. K. 1968. Lower Cretaceous Trigoniidae from Stanwell, eastern Queensland. *Bulletin. Bureau of Mineral Resources, Geology and Geophysics, Australia* **80** (Palaeontological Papers, 1965): 167–180.

SKWARKO, S. K. 1970. An Upper Jurassic *Apiotrigonia* from Mexico. *Boletín de la Sociedad geologica mexicana* **31** (2): 75–78.

SPATH, L. F. 1927–1933. Revision of the Jurassic cephalopod fauna of Kachh (Cutch), 1–6. *Memoirs of the Geological Survey of India, Palaeontologia indica* **9** (2): vii, 1–955.

SPATH, L. F. 1935. On the age of certain species of *Trigonia* from the Jurassic rocks of Kachh (Cutch). *Geological Magazine* **72** (850): 184–189.

STEINMANN, G. 1882. Die gruppe der Trigoniae pseudoquadratae. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* **1**: 219–228.

STOLICZKA, F. 1870–1871. Cretaceous faunas from southern India. III. The Pelecypoda, with a review of all known genera of this class, fossil and recent. *Memoirs of the Geological Survey of India. Palaeontologia indica* (6) **3**: 1–537.

STOYANOW, A. 1949. Lower Cretaceous stratigraphy in southeastern Arizona. *Memoirs. Geological Society of America* **38**: 1–169.

TASHIRO, M. 1979. A study of the 'pennatae trigoniids' from Japan. *Transactions and Proceedings of the Palaeontological Society of Japan* (n.s.) **116**: 179–222.

TASHIRO, M. 1988. Notes on '*Trigonia deckeina* Kubota' from the Cretaceous of Hokkaido. *Memoirs of the Faculty of Science, Kochi University* (E, Geology) **9**: 11–14.

TASHIRO, M. & KANO, M. 1989. On a new species of *Yaadia* (Cretaceous trigonian) from Kyushu, Japan. *Memoirs of the Faculty of Science, Kochi University* (E, Geology) **10**: 7–12.

TASHIRO, M. & MATSUDA, T. 1986. A study of the Pterotrigoniae from Japan. II. Morphological changes. *Memoirs of the Faculty of Science, Kochi University* (E, Geology) **7**: 1–18.

TASHIRO, M. & MOROZUMI, Y. 1982. Late Cretaceous knobby trigonians from the Izumi Mountains, southwest Japan. *Bulletin of the Osaka Museum of Natural History* **36** (260): 1–8.

TATE, R. 1867. On some secondary fossils from South Africa. *Quarterly Journal of the Geological Society of London* **23**: 139–174.

WILLEY, L. E. 1973. Belemnites from south-eastern Alexander Island: II. The occurrence of the family Belemnopseidae in the Upper Jurassic and Lower Cretaceous. *Bulletin. British Antarctic Survey* **36**: 33–59.

WOODS, H. 1917. The Cretaceous faunas of the north-eastern part of the South Island of New Zealand. *Palaeontological Bulletin. New Zealand Geological Survey. Wellington* **4**: 1–41.

VAN HOEPEN, E. C. N. 1929. Die krytfauna van Soeloeland. 1. Trigoniidae. *Paleontologiese Navorsing van die Nasionale Museum van Bloemfontein* **1** (1): 1–38.